Vol. 6, No. 2 November, 1937

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THE JOURNAL OF ANIMAL ECOLOGY

EDITED FOR THE
BRITISH ECOLOGICAL SOCIETY

by
CHARLES ELTON
and
A. D. MIDDLETON

LONDON
CAMBRIDGE UNIVERSITY PRESS
BOMBAY, CALCUTTA, MADRAS: Macmillan
TOKYO: Maruzen Company Ltd.

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Annual subscription: thirty shillings (twenty-five shillings to members of the British Ecological Society)

PRINTED IN GREAT BRITAIN

World-List abbreviation: J. Anim. Ecol.

THE JOURNAL OF ANIMAL ECOLOGY

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STUDIES IN NOCTURNAL ECOLOGY

FURTHER ANALYSIS OF ACTIVITY IN THE BEETLE, *PASSALUS CORNUTUS*, AND DESCRIPTION OF AUDIO-FREQUENCY RECORDING APPARATUS

BY ORLANDO PARK

(*Northwestern University, Illinois, U.S.A.*)

(*With Plate 7 and 5 Figures in the Text*)

1. INTRODUCTION

ALTHOUGH the physiology of animal motility has been the subject of searching investigation, inadequate attention has been paid to the physiological problems arising from the fact that some animals move about only during daylight hours, others only at night, and still others appear to be uninfluenced by the changing conditions of the diurnal cycle.

A more rigorous study of environment has been made possible by application of a rapidly increasing array of experimental techniques. However, many of the earlier ecological principles had been based on data collated in the study of diurnal animals. Therefore such ideas remain at best half proven, since the nocturnal constituents of a community are both abundant and important.

A preliminary field study of nocturnal animals was conducted some years ago (Park, Lockett & Myers, 1931) and it was found that the distribution and amount of activity appeared to be correlated with the expression of the environmental influences operating at night. Such field work has been extended (Carpenter, 1935; Park & Strohecker, 1936; Park, 1937) and the activity of individuals compared both in the field and under controlled laboratory conditions (Park & Sejba, 1935).

However, when such forest forms were subjected to laboratory experimentation it was found that not all species had such a close dependence upon environment. In general, species activity was specific and divisible into the following categories:

(1) Environmental type: activity apparently controlled by the operating environmental influences, having consequently an apparent activity rhythm induced by the rhythmic day-night cycle, e.g. *Parcoblatta pennsylvatica* (Park & Keller, 1932) and probably *Crotalus cerastes* (Mosauer, 1936).

(2) Inherent type: activity apparently more deeply seated in the protoplasm, hence innately rhythmic and the basic periodism less subject to

destruction by experimental alteration of the environmental influences, e.g. the rodents, *Peromyscus*, *Microtus*; and the insects *Gryllus*, *Stenopelmatus*, *Spirobolus*, *Boletotherus*, *Megalodacne* and certain Saturniid moths (Johnson, 1926; Rau & Rau, 1929; Lutz, 1932; Park & Keller, 1932; Davis, 1933; Park, 1935; Park & Sejba, 1935). It is interesting to note again the parallel between inherent activity of the species, and the deeply seated physiological rhythm of the Reptilian heart (Chu & Sollmann, 1925 *a* & *b*), the migration of pigment in Crustacean eyes as indicated in the important work of Welsh (1930 *a* & *b*) and Bennitt (1932 *a* & *b*) and the theory of hormone regulation which has been suggested by the work of Perkins (1928) and Perkins & Kropp (1932) and Kleinholz (1934).

(3) Arhythmic type: activity having no discernible periodicity and consequently evenly distributed over the 24 hr. cycle, e.g. *Passalus cornutus* (Park, 1935; Pearse, Patterson, Rankin & Wharton, 1936) and possibly many species of ants (Flint, 1914; Park, Lockett & Myers, 1931; Park & Strohecker, 1936).

(4) Composite type: recent work in this laboratory indicates a fourth form of general activity, in which at least two of the above types may be operating together to form the activity pattern of a species, e.g. certain crayfish (Park & Roberts, 1937).

In these studies, several types of recording apparatus have been devised to render the accumulation of data objective. The effect of varying certain influences, while holding others stable, has been studied, e.g. intensity of light, hunger, aggregation. Finally, the significance of these findings to general biological problems has been discussed elsewhere.

The audio-frequency recording equipment described here was made possible by a research grant from Northwestern University and the writer is happy to acknowledge his further indebtedness to Mr A. W. Krause for his engineering skill in the construction of the apparatus; I also wish to express appreciation to Professors W. C. Allee and J. W. Buchanan for timely criticism. This is the sixth report in a study of nocturnal ecology.

2. Further analysis of activity in *Passalus cornutus*

By means of recording apparatus described previously (Park, 1935) it was demonstrated that the activity of the black Passalid, *Passalus cornutus* Fab., was so distributed over the 24 hr. day-night cycle that no periodicity was apparent. In these trials single beetles were placed under conditions of total, constant darkness, a constant air temperature of 22·6–24·6° C., and a saturated atmosphere.

This third category of activity, the arhythmic type, presented so many interesting features for analysis that another series of experiments was devised to study this aspect of the general problem of nocturnal ecology. The amount of illumination was the first influence to be varied. In the following table

(Table 1) the data taken are given under three differing amounts of illumination: (1) total darkness, (2) constant light (29–30 foot-candles), and (3) reversed illumination (29–30 foot-candles during the night, and total darkness during the day). Single beetles were used for each trial and each marked differentially. 13 of the 15 trials were of 24 hr. duration; one individual (male, NU 2–1) was weak at the beginning of the trial and died after 8 hr., and another beetle (female, NU 7–1) had just pupated and was so weak that moderately little activity was recorded; the animal died after 20 hr. The cabinet air temperature varied from 21 to 25° C. for the 15 trials, but with a maximum variation of 2° and a minimum variation of half a degree per trial. The total variation of 5° may be attributed to two factors: the lag in the cabinet thermostat over a period of varying weather conditions from January to November, 1935, and the difficulties involved in holding a constant temperature under three different degrees of illumination while varying relative humidity within the cabinet.

Table 1. *Activity of* Passalus cornutus

Trial	Total time hr.	Total active time hr. min.	Total inactive time hr. min.	Total day activity hr. min.	Total night activity hr. min.
		Constant darkness			
NU 2–1	8	5 47	2 13	3 34	2 13*
NU 3–1	24	20 27	3 33	11	9 27
NU 5–1	24	22 59	1 1	10 59	12
NU 7–1	20	5 44	14 16	2 4	3 40
NU 11–1	24	21 17	2 43	9 22	11 55
Totals	100	76 14	23 46	36 59	39 15
		Constant illumination			
NU 1–1	24	22 55	1 5	12	10 55
NU 4–1	24	23 50	10	11 50	12
NU 5–2	24	22 28	1 32	11 26	11 2
NU 6–1	24	21 44	2 16	11 44	10
NU 11–2	24	16 48	7 12	8 3	8 45
Totals	120	107 45	12 15	55 3	52 42
		Reversed illumination			
NU 8–1	24	17 10	6 50	8 45	8 25
NU 9–1	24	18 33	5 27	9 14	9 19
NU 10–1	24	21 42	2 18	11	10 42
NU 11–3	24	23 16	44	11 38	11 38
NU 12–1	24	20 58	3 2	10 45	10 13
Totals	120	101 39	18 21	51 22	50 17

Tabulation of percentages

	Time active %	Time inactive %	Day activity %	Night activity %
Constant darkness	76	24	48	52
Constant illumination	90	10	51	49
Reversed illumination	85	15	51	49

* Died during experiment.

From the data in Table 1 it is obvious that the activity of *P. cornutus* is equally distributed between day and night. Furthermore, the percentage of activity is not appreciably changed whether the beetles are in total darkness, under constant illumination of 29–30 foot-candles, or under the abnormal conditions of reversed illumination. To illustrate further the aperiodicity of the species, under the experimental conditions used, three graphs are presented. They represent three trials of the same individual, taken within a limited number of days so that individuality of behaviour and physiological condition are minimized. In all three the air temperature of the cabinet was held between

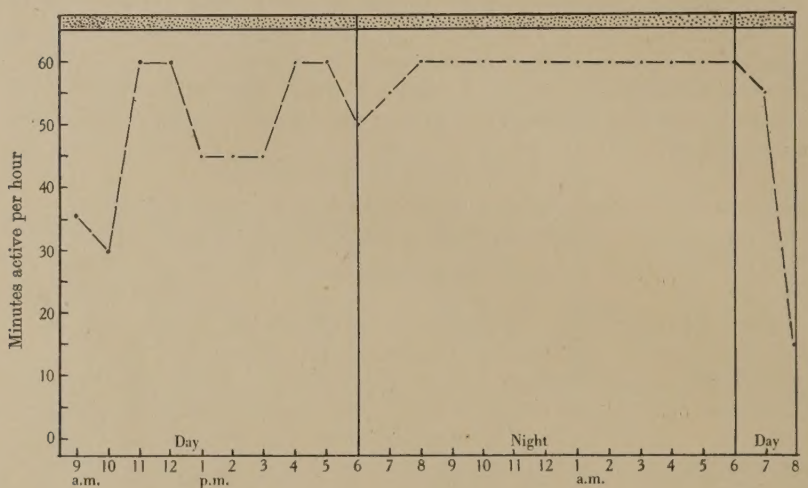

Fig. 1. Activity of *Passalus cornutus* (NU 11–1), 15–16 July. Constant darkness (stippled bar at top of graph); air 23–25° C.; relative humidity 65–75%.

23 and 25° C., and the relative humidity (R.H.) between 65 and 75%. The amount of light varied, one trial in constant darkness (Fig. 1), one in 29–30 foot-candles (Fig. 2), and one in reversed illumination (Fig. 3). No two curves are identical, nor is any one a pattern for other trials in Table 1. Thus Fig. 2 is quite irregular, but other trials of other individuals under identical conditions gave a much higher, more constant average activity.

The bearing of this arhythmic activity upon the autecology of this species, and its probable significance has been discussed previously (Park, 1935); these further trials merely substantiate the earlier results in which the condition of total darkness obtained. As was said earlier, the time of year, time of start of the trial, familiarity with the apparatus as indicated by trial sequence, and the interval spent in the laboratory have no appreciable effect upon activity. It can be stated further that the original source of material does not appear to be important, since individuals have been used which came from logs in

Mississippi, Illinois, Indiana and Arkansas. Furthermore, the sex of the animals, determined by dissection of the reproductive tract after death, does not seem to bear upon the degree or distribution of activity.

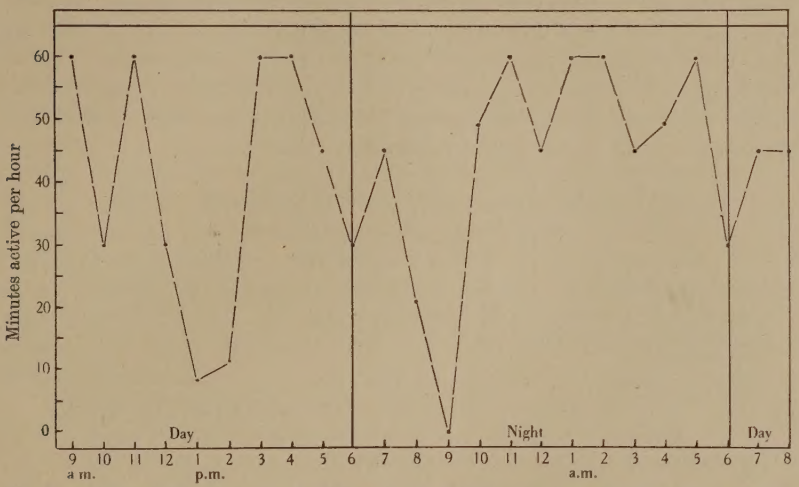

Fig. 2. Activity of *Passalus cornutus* (NU 11–2), 17–18 July. Constant illumination (29–30 foot-candles), otherwise as in Fig. 1.

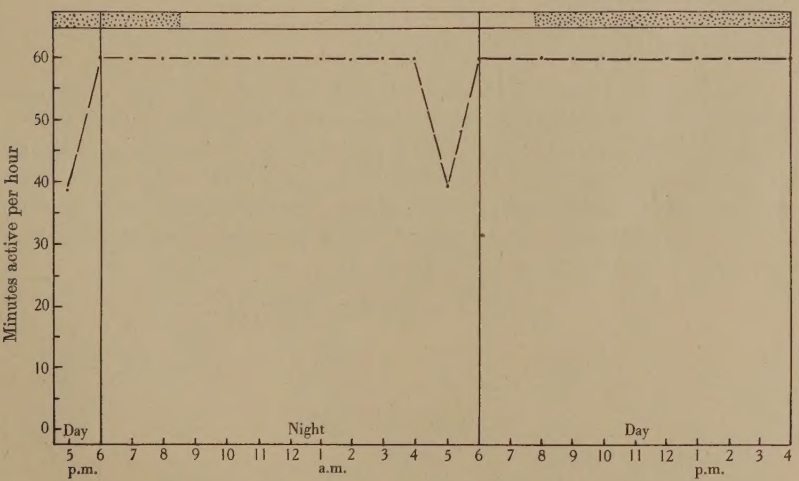

Fig. 3. Activity of *Passalus cornutus* (NU 11–3), 22–23 July. Reversed illumination (stippled bar at top of graph denotes period of total darkness), otherwise as in Figs. 1 and 2.

After evaluation of illumination as a factor, the relation between R.H. and activity remained undetermined; this was the second influence which was

studied, especially since such investigation might have a bearing upon the species' reactions in their natural habitat. In the work reported previously the atmosphere was held at or near saturation. In the trials reported in Table 2 the R.H. of the cabinet was varied over the experimental range of 17–77%. In any one of these trials the average variation in the R.H. was 5%. Now when we contrast the totals of the trials run at or near saturation-point with those at much lower R.H., we find that there is a notable average increase in total activity with decrease in R.H. This general relationship is shown in Table 2, where the two groups of trials are contrasted.

Table 2. *Effect of decreased relative humidity on activity*

(Single *Passalus cornutus* for 24-hr. trials)

	Data from Park, 1935	Data from present report
Animal experimental hours	312	340
Range of air temperature	22·6–24·6° C.	21·0–25·0° C.
Maximum range of temperature per trial	3·5	2·0
Type of illumination	Total darkness, 13 trials	Total darkness, 5 trials Constant light, 5 trials (29–30 foot-candles) Reversed light, 5 trials
Relative humidity	95–100%, 13 trials	17–29%, 1 trial 24–38%, 1 trial 30–35%, 9 trials 65–77%, 4 trials
24 hr. average activity	10·3 hr.	19·0 hr.
Average nocturnal activity	4·7 hr. (46%)	9·4 hr. (50%)
Average diurnal activity	5·6 hr. (54%)	9·6 hr. (50%)

This interesting lead was followed by a new series of trials. For these a new stock of animals was obtained from Arkansas and isolated from other experimental colonies in a large container supplied with an abundance of moist, well-decayed log fragments. Differentially marked individuals were placed in the apparatus for isolated 24 hr. trials. These trials were run in total, constant darkness and a cabinet temperature of 20–21° C., but with a R.H. which varied for the series between 20 and 95% (Table 3).

Table 3. *Activity of* Passalus *at varying humidities*

Trial	Total time hr.	Total activity hr. min.	Day activity hr. min.	Night activity hr. min.	Relative humidity %
NU 50	24	20 8	8 43	11 25	20–30
NU 51	24	13 45	8 35	5 10	80–85
NU 52 (1)	24	20 55	8 55	12	80–85
NU 52 (2)	24	11 40	5 25	6 15	80–85
NU 98	24	14 27	6	8 27	80–90
NU 99	24	14 15	6 10	8 5	80–90
NU 100 (1)	24	21 30	10 55	10 35	69–77
NU 101	24	22 20	11 30	10 50	55–56
NU 100 (2)	24	10 40	5 40	5	86
NU 102	24	11 35	8 30	3 5	86
NU 103	24	11 35	6 40	4 55	86

Of these 11 additional trials with a new stock of animals, 10 were spaced from 2 to 4 days apart so that where the same individual was used in more than one trial, in the interval the animal was enabled to feed and lead a relatively normal existence. The second trial of number 52, however, was continuous with the first trial; the animal was recorded for 48 consecutive hours. It will be noted that, though in the first trial the beetle was exceptionally active at the R.H. used, the activity fell markedly during the second period. This illustrates the effect of fatigue upon activity; the same effect has been observed upon numerous other occasions.

The 10 trials in which individuals were taken from the log mould in presumably good physiological condition, however, demonstrate again that there is a general decrease in activity with increase in R.H., other influences being held within normal limits. Secondly, the trials show once more that there is a high degree of individual variability of response, as is to be expected in an arhythmic form. Thus, although the individual trials favour a diurnal or a nocturnal preponderance of activity, this individual difference vanishes in the averages.

Another way in which the individuality of behaviour can be considered is the following: from Table 3 we see that of the 11 trials, 5 show more nocturnal movement, and 6 more diurnal activity. If the net difference in minutes is calculated for each trial by subtraction, and these differences added, it will be seen that there is a nocturnal balance of 10 hr. 59 min. for 5 trials, and a diurnal balance of 11 hr. 15 min. for 6 trials. This means that there is only a net difference of 16 min. in favour of diurnal activity for 264 animal experimental hours! Such a result confirms the earlier conclusion that in this species the activity is equally distributed over the 24 hr. period.

The general trend of activity with respect to R.H. is expressed graphically in Fig. 4. This is obtained by plotting total hours active against the R.H. range for the 10 trials noted in Table 3; secondly, the 15 trials listed in Table 1, in which both degree of illumination and R.H. were varied; thirdly, the 13 trials run in constant darkness and saturated atmospheres previously reported (Park, 1935). The second group of trials is included, since a comparison of the averages shows no appreciable constant difference in activity between the degrees of illumination used.

This graph of the species' activity as a whole does not show a sharp and definite response to differing R.H., but does indicate a definite trend of decreased activity with increased R.H. Assuming that the humidity effect is transmitted to the organism through the medium of the respiratory system, for further elucidation of this problem we must consider spiracle physiology.

Leaving this for future work, and considering the response *per se*, we suggest that this has a bearing upon the normal autecology of the species. *P. cornutus* is a social, dendrocolous species, which has been recently monographed by Pearse, Patterson, Rankin & Wharton (1936). A more or less closely integrated

society inhabits a fallen log or stump. In these habitats the wood is usually well decayed and easily galleried, and, in my experience, the wood is generally quite moist. In such an environment the beetles would be in total darkness. Since the logs are found normally upon the floors of subclimax or climax forests, they are deeply shaded by the canopy during the season of foliation; consequently the internal log temperatures must be relatively stable as contrasted with the air temperatures in the shaded forest. Finally the galleries and chambers in the moist, soft wood probably have a high R.H.

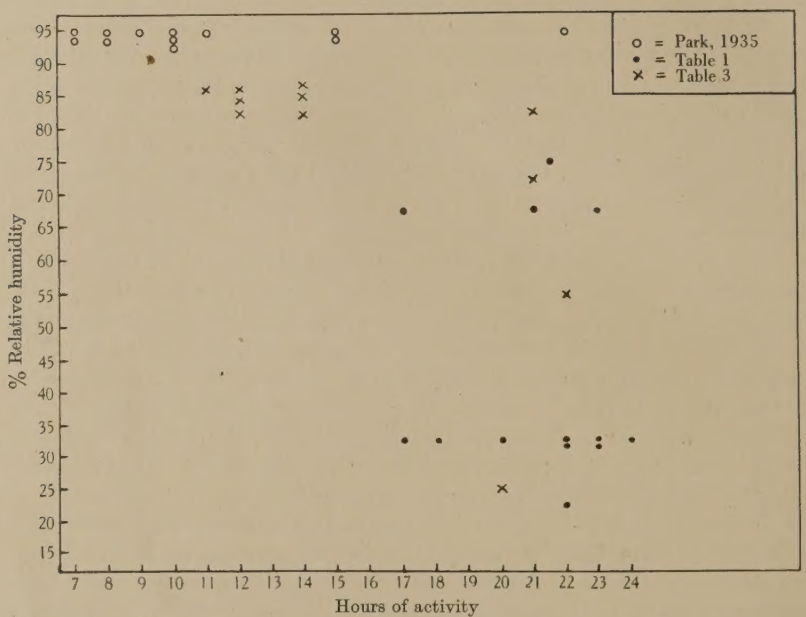

Fig. 4. Relation of total average activity of *Passalus cornutus* to percentage of relative humidity.

Under these normally stable conditions, then, the soil temperature (McColloch & Hayes, 1923) as well as the prostrate log internal temperatures (Graham, 1920, 1925) would tend to lag behind air temperature, and the air temperatures of the shaded forest floor would be such that extreme log temperatures would be very rare. This favourable temperature range would tend to conserve log moisture, and consequently favour high R.H. in the beetle's burrows. Since high R.H. have been shown to be optimal for many phases of insect development and ecology (cf. Chapman, 1926), it would seem that *P. cornutus* carries on its existence under optimal conditions. Such conditions are approximated by the experimental conditions employed previously (Park, 1935). If the data taken can be used to evaluate normal

activity of the species, then we should expect the adults to average about 10 active hours out of 24, with about half of this period falling in the day and half during the night.

This normal routine should persist as long as the food supply remains and the operating influences are tolerable. But if the food supply is exhausted by long continued tunnelling, the log would become less constant in its temperature and moisture content; or if the log were destroyed the galleries would be broken and the amount of moisture present would be rapidly dissipated. When the damaged habitat finally became untenable the adults would move out in search of another log, and, presumably by trial and error, the movement would continue until another habitat was found which satisfied their requirements.

In our opinion, the data obtained in the present report tend to clarify this sequence of events. Under the winter range of temperature the species would be dormant, but if the habitat were damaged in the spring, summer or early autumn, the temperature would favour increased activity. Therefore with tolerable temperature, the animals would have their average activity greatly augmented by the greatly diminished R.H. of their anastomosing galleries. This increased activity, of course, would not necessarily tend to stimulate a migration away from the site of activity. If such a migration was initiated, the increased activity might presumably make a more rapid occupation of another habitat niche possible. Further, since the species is arhythmic in its activity, the amount of light or darkness present would not markedly disturb its movements; it could work at night as well as during the day. If the finding of another suitable habitat niche is necessary for the species, then the rapidity with which this is found is important. It would seem that increased activity which comes with increased temperature and lower relative humidity, coupled with the arhythmic distribution of activity over the 24 hr. cycle, in part at least, explains the ability of *P. cornutus* to maintain its place in more mature associes of the forest sere.

3. Description of recording apparatus, and its use in checking the activity of *Passalus cornutus*

The recording equipment previously described has proved to be both accurate and reliable but open to the following objections: (1) An activity record could be obtained of only one individual at a time, unless one were dealing with a species with an inherent activity rhythm such as *Megalodacne heros* (Park & Sejba, 1935), where the group tended to be active or inactive at the same general time. In such arhythmic forms as *Passalus cornutus* the group record did not give a clear picture of amount of movement. (2) The accumulation of faeces occasionally unbalanced the disk of the apparatus. (3) The equipment was not sensitive enough to record the movements of

minute forms, nor to measure in any way sounds such as stridulation. (4) Operation of the secondary circuit in making the record was not noiseless. (5) These four objections are not critical, but finally the equipment made it necessary to record the activity of an animal on a metal surface, and consequently a natural environment could not be provided.

All five of these objections have been overcome by the construction of new recording apparatus which utilizes an entirely different mechanism. This is an audio-frequency machine, in which even minute sounds or vibrations are made audible by four stages of amplification. Thus the wing vibration of house-flies or the stridulation of *P. cornutus* may be made painfully audible. The stridulation of the adult *cornutus* was measured on a Triumph Oscillograph, Model 800, and found to be between 4000 and 5000 cycles per sec., so that the ultimate range of this equipment remains unrealized.

Such a device opens up a vista of problems. In the first place, activity rhythms of much more minute species can be studied, and the increasing interest of biologists in inherent rhythms can be served where the inherent activity is the phase being investigated. Secondly, the equipment makes possible the recording of the sounds made by animals, and consequently the subject of communication in insects, such as the stridulating Orthoptera, many beetles, etc., can be further analysed. Among social insects, the possibility of communication is interesting. Both the larvae and adults of *P. cornutus* have stridulatory mechanisms, and it has been demonstrated by Emerson & Simpson (1929) that the soldiers of at least some species of termites drum with their heads upon the walls of their galleries. It is hoped that the recording equipment will open up new possibilities in other types of biological investigation.

A detailed description of the equipment is rendered unnecessary by the wiring diagram (Fig. 5). The completed apparatus is shown in Plate 7, phot. 1. The top half of the encased equipment holds the several indicators of activity, viz. loud speaker, which can be switched in or out of circuit at will, secondly the visual indicator, a small bulb which lights momentarily with each movement of the experimental animal, and thirdly the relay pen which makes a continuous record of activity, or other sounds, upon a strip of waxed record

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EXPLANATION OF PLATE 7

Photo. 1. Audio-frequency recording apparatus. Weight, 65 lb. *a*, loud-speaker. *b*, toggle-switch for throwing loud-speaker in or out of circuit. *c*, visual indicator (small bulb). *d*, relay, carrying pen or tambour. *e*, aluminium drum carrying red backed waxed paper, and driven by a 24 hr. Taylor clockworks. *f*, output line. *g*, 22·5 V. battery. *h*, sensitivity control. *i*, volume control. *j*, microphone or input line. *k*, power line, 110 V., 60 cycles. *l*, No. 80 tube. *m*, thyratron tube. *n*, No. 45 tube. *o*, No. 53 tube. *p*, No. 57 tube.

Photo. 2. Two trials of groups of *Passalus cornutus* with combined activity recorded by the audio-frequency equipment. Note how the varying and overlapping periods of activity of this arhythmic species have produced a group record of continuous activity.

Photo. 1 (*see opposite page*)

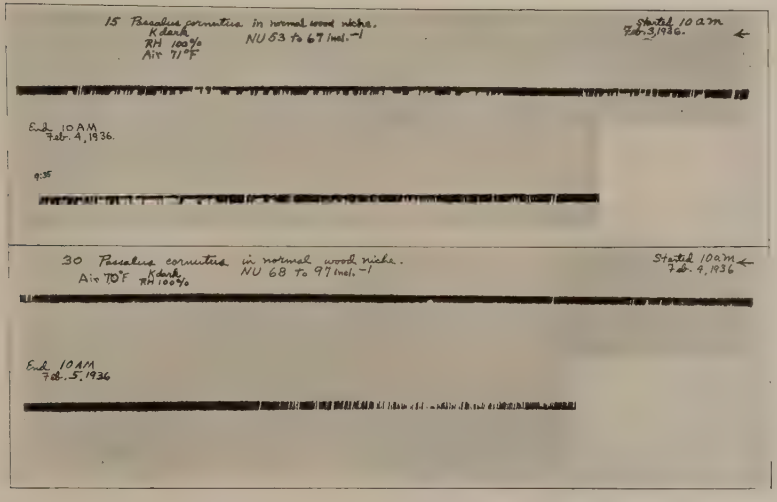

Photo. 2 (*see opposite page*)

PARK—NOCTURNAL ACTIVITY

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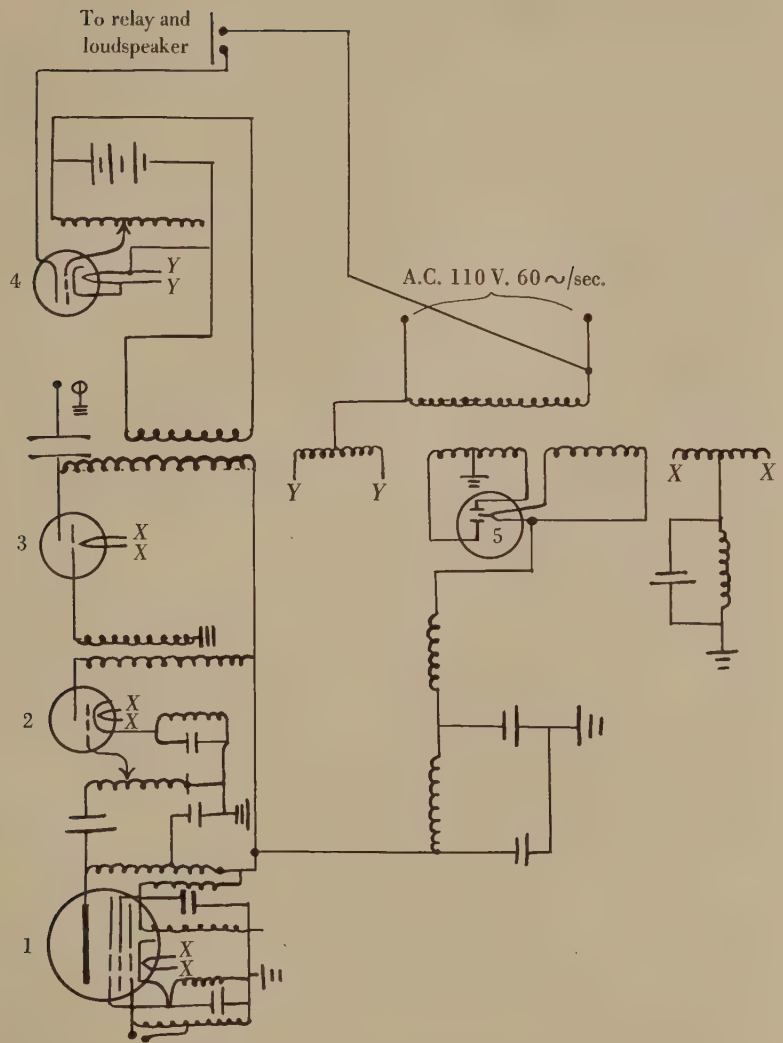

Fig. 5. Diagram of audio-frequency recording apparatus, using international symbols. Tubes: 1. Pentode tube, No. 57. 2. Double-plate double-grid tube, No. 53. 3. Power amplifier tube, No. 45. 4. Thyratron tube, special. 5. Rectifying tube, No. 80.

paper. This latter is carried upon a drum driven by a 24 hr. clockwork; or an electrically driven clock can be used.

The whole apparatus weighs 65 lb. and consequently is portable. In the laboratory where analyses of activity are to be investigated under controlled conditions, the matter of insulating the experimental animals and the delicate microphone from external sounds or vibration is of the greatest importance.

The container can be of any size, depending upon the number of animals and size of species to be used, and the extent to which the natural habitat is to be simulated. However, we have been interested especially in another of the three types of activity, the inherent type. In the analysis of this latter form of periodism it is essential that the environment be held perfectly constant. In so far as the ordinary influences are concerned, e.g. light, temperature, R.H., rate of evaporation and air movement, these factors have been held within experimental limits (Park & Keller, 1932; Park, 1935; Park & Sejba, 1935). Within recent months, however, interest has been focused upon a number of other entities which may have to be coped with in the standardization of environment, viz. cosmic rays; short-wave radio; size and number of ions in the atmosphere; and infra-red waves.

All or any of these little understood disturbances, if they are proven to have a definite seasonal march, or especially if a diurnal-nocturnal variation can be demonstrated, may become of importance in the evaluation of the inherent activity rhythm. A specially constructed experimental chamber was made up to eliminate infra-red wave variation. This is a double-walled box, the interior measuring $12 \times 12 \times 12$ in. Within the latter is a small container 1 in. wide and 6 in. high to accommodate the microphone. Thus the inner box can be supplied with soil, log wood, etc., and the activity of the animals can be recorded in a relatively natural substratum, without the microphone becoming clogged with particles of soil or wood.

The outer box is 2 in. longer in each dimension. The inner box is placed on a thick layer of insulating cotton, cotton stuffed between the walls, and the two boxes are then sealed permanently. The cover is also double-walled, with the space between the two tops similarly filled with cotton; the outer cover is sufficiently deep to fit tightly over the sealed walls of the container. This construction provides a light-tight, well-insulated inner chamber. The whole box, both inner and outer walls and covers, is made of heavily lead-coated tin, and the sealing done with thick solder.

The box is then given three wrappings of cloth, alternating with three layers of sheet cotton and the whole placed in a large cabinet on rubber pads to eliminate violent vibrations or shocks. The large cabinet may be a wooden or lead-lined wooden box, or an electric refrigerator, depending upon the nature of the experiment.

To avoid cosmic rays, of course, the recording equipment would have to be installed in a cabinet with lead walls of great thickness. Since this is

usually prohibitive, work is now being planned in which records are to be made in Mammoth Cave, Kentucky, where the great depth of the lower tunnels (350 ft.) will presumably serve the same purpose.

The audio-frequency recording equipment and cabinet are described at this time since the former was used to re-check the data presented in the first part of the present report. It was shown previously (Park, 1935) that *P. cornutus* was arhythmic, that is, has its activity distributed over a 24 hr. period under controlled conditions, but with the individuals of the species having a highly individual and irregular behaviour. These conclusions were substantiated in the first part of the present paper, both series of experiments being recorded by equipment described in 1932 and 1935. The present apparatus, however, could record numbers of individuals at the same time, and give a record of the group's combined activity.

The species is so arhythmic that the individuals are never all active nor all inactive for any length of time, and consequently the activity of the group should give a record of virtually continuous activity if our previous conclusions are correct. Two lots of *P. cornutus* were used. Each group was recorded in its normal habitat of moist, soft log wood in a constant temperature and total darkness; the trial was of 24 hr. duration to coincide with earlier experiments, and to avoid any possible fatigue factor, although the latter was not to be looked for in the present more natural environment. The first lot consisted of 15 beetles (NU 53-67), and the second lot of 30 beetles (NU 68–97). The results are shown in the accompanying Plate 7, phot. 2: both records are of practically continuous activity. Incidentally, this also shows the possible fallacy of drawing conclusions as to the activity of the individual from the activity of the group as a whole. This is less the case, of course, where the rhythm of the species is demonstrably in the inherent category, and where all of the individuals tend to respond in the same way at the same time, but is certainly the case in the arhythmic forms.

4. SUMMARY

1. The subsocial, log-inhabiting beetle *Passalus cornutus* Fab. is arhythmic, that is, its activity is equally distributed over the 24 hr. period under relatively constant environmental conditions. Furthermore, under these stable conditions there is a large amount of individual arhythmic activity but with the average activity equally distributed between day and night.

2. In experiments conducted in the laboratory within normal spring-summer limits of temperature, activity distribution is not influenced apparently by time of year, time of start of trial, trial sequence, interval spent in the laboratory, geographic source of material, or sex.

3. Arhythmic activity was not appreciably altered by constant darkness (normal for the species), constant light (29–30 foot-candles) or reversed illumination.

4. Distribution of average activity was not altered by change in relative humidity, but there was a definite effect upon average amount of activity with change in R.H. In R.H. at or near saturation, activity was relatively low (8–12 hr. per day-night period), and with decrease in R.H. there was a definite but gradual increase in activity.

5. Fatigue was accompanied by marked decrease in amount of activity in the second 24 hr. period of a 48 hr. trial.

6. The bearing of these data upon the normal autecology of the species is discussed and an explanation offered.

7. A new recording apparatus is described and its use discussed. This latter equipment is based upon the audio-frequency principle.

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SOME PHYSIOLOGICAL ADAPTATIONS OF THE MOUNTAIN AND PLAIN FORMS OF THE WOOD-MOUSE (*APODEMUS SYLVATICUS*) AND OF OTHER SPECIES OF MOUSE-LIKE RODENTS

By N. J. KALABUCHOV

Laboratory of Ecology, Zoological Institute, Moscow University

(*With 4 Figures in the Text*)

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1. Introduction

Every new character appearing in animals as a result of the process of evolution may prove to be useful, injurious, or indifferent for the existence of a given species. These characters in their turn determine the further course of natural selection. Therefore the study of the adaptive significance of species characters is of theoretical interest. Different methods might lead to the solution of this problem. Thus, for instance, one can study different characters of nearly related forms of animals, and, having compared them with the conditions of the environment, in which these organisms live, establish the adaptative role of these differences. Inversely, one can take beforehand such characters as are undoubtedly of an adaptative importance and trace their presence or absence in forms dwelling in different ecological conditions. In the present work we have endeavoured to study in this way one of the adaptive characters of mammals, namely the differences in the composition of the blood of mountain and plain rodents.

A number of investigations made on human beings (see Barcroft, 1925; Loewy, 1932; Haldane & Priestley, 1935) and on laboratory animals (see, for instance, Abderhalden *et al.*, 1937; Loewy, 1932) have shown that on

ascending mountains the content of haemoglobin and number of erythrocytes in the blood increased. This fact was usually taken as an example of an accommodation of the organism to unfavourable conditions—namely to a reduced oxygen pressure. A comparison of these indicators in wild mountain mammals (marmots (Abderhalden *et al.*, 1927); viscachas and guanacos (Hall *et al.*, 1936); lizards (Richter, 1933) and in the natives of mountain regions (Barcroft, 1925; Hurtado, 1932)) also made it apparent that in the mountain forms the blood capacity as regards oxygen, viz. the quantity of haemoglobin and number of erythrocytes (per unit of blood volume), is higher than in animals which inhabit plains.

It was also recognized that an increase of these indicators in animals of the plains with an ascent into the mountains is only a temporary reaction, a descent to the sea-level being accompanied by a diminution of the quantity of haemoglobin and of the number of erythrocytes down to the former level (Barcroft, 1925; Grollman, 1930; Haldane & Priestley, 1935). In order to establish whether the difference in these indicators in animals constantly dwelling in the mountains is also the result of a direct action of the external medium, it was necessary to transport the mountain animals or human mountain dwellers into the plain. Experiments of this kind have been made with lizards (Richter, 1933) and marmots (Abderhalden *et al.*, 1927). These investigations have shown that after the transfer of the animals into the plain (after 4–6 weeks for lizards, and 6–7 weeks for marmots) their haemoglobin content and number of erythrocytes diminishes, although it does not fall to the level typical for the forms of the plain.[1] However, the data of Abderhalden *et al.* concerning marmots may not be characteristic for other mammals, as in the summer and autumn periods sharp changes connected with their hibernation take place in the blood of these rodents. Therefore the results of these researches which seem to prove that the physiological differences of mountain animals may depend principally on the direct action of the external medium, do not take account of a number of other possibilities.

Particularly, it appeared probable that in other cases these physiological peculiarities can be independent of external conditions and become fixed in mountain animals as in ecological subspecies or races. This raised the question of a more detailed study of these differences in the mammals of the mountain and the plain. In 1934–6 I carried out a number of investigations and experiments on this subject.

2. MATERIALS AND METHODS

The work was carried out chiefly with wood-mice (*Apodemus sylvaticus* L.) taken in the mountain region of the Caucasus at a height of 1500–1800 m. (Gondoray and Arkhys, see Fig. 1). By their morphological characters the

[1] Hingston transferred the inhabitants of high mountain regions in the Himalayas from an altitude of 3300 m. to an altitude of only 2500 m. above sea-level.

rodents from these places belong to the ante-Caucasian subspecies (*A. sylvaticus ciscaucasicus* Ogn.). For comparison an investigation was made of mice from the plain region of the Northern Caucasus (Nevinnomysskaja, height 300 m.)

Fig. 1. Sketch-map of European part of U.S.S.R. The black dots show the origin of plain and mountain rodents investigated.

belonging to the same subspecies. Likewise investigations were regularly made on the mice of the plain from the environs of Moscow, belonging to another subspecies (*A. s. mosquensis* Ogn.).

Material was also received for a number of experiments and for the precipitation reaction from some other mountain parts of the Caucasus (Utchkulan.

and Teberda, about 25 km. from Gondoray and Arkhys), and from the North Caucasus plains (Voroshilovsk, 60 km. from Nevinnomysskaja).

The following determinations were made in the mice:

(1) The haemoglobin content, by the method of Sahli.

(2) The number of erythrocytes, by counting in a Bürker-Türck counting chamber.

(3) Size of the erythrocytes, from measurement on smears.

The animals were weighed and their age and sex were also determined. Blood was taken from the tail, so that the same animal could be used several times for investigation. The method of estimating blood counts was as follows. The blood was taken at each observation into two "mélanger" pipettes in a dilution of 1/200, and sample counting from each pipette done on 80 cells of a Bürker-Türck counting chamber (volume of each 1/4000 mm.^{3}) was carried out. By this means 800–1000 erythrocytes were actually counted from each pipette (for different mice and different regions), i.e. from 1600 to 2000 red blood cells for each comparison (or 160 cells of the counting chamber). Since it is known that the error in counting 16 cells of the counting chamber is equal to 5% of the estimated value, and for 100 cells only 2%, these figures mean that a difference in blood cell count of more than 150,000–200,000 has significance for the investigation. In order to establish the influence of a change of altitude of the habitat upon the indicators studied, a number of experiments were made.

3. Physiological peculiarities of the mountain and plain forms

First of all we proceeded to a study of the physiological differences in the wood-mice (*A. s. ciscaucasicus*) from the plain regions of the Northern Caucasus and in the mountain *A. s. ciscaucasicus*. This study, conducted under the conditions of the expeditions in the summer of 1934 and 1935, yielded interesting data. It appeared that the haemoglobin content and the numbers of erythrocytes in the mountain *A. s. ciscaucasicus* from a height of 1500–1800 m. (Gondoray and Arkhys) is 9–12% higher than those of the plains (see Table 1).

Table 1. *Number of erythrocytes and haemoglobin content in the blood of wood-mice from the mountains and of the plain of the Northern Caucasus, belonging to one subspecies* (A. s. ciscaucasicus *Ogn.*)

	Haemoglobin content		No. of erythrocytes per 1 mm.^{3} of blood	
	No. of mice	Mean (and S.E.)	No. of mice	Mean
Plain mice	14	97·0 ±2·37	28	8,746,407 ±161,003
Mountain mice	26	108·8 ±1·89	41	9,539,170 ±135,539
Mountain mice: % difference from plain mice	26	112·1	41	109·0

We also compared the peculiarities of blood composition in plain mice from the environs of Moscow belonging to another subspecies (*A. s. mosquensis* Ogn.) and that of mountain *A. s. ciscausacicus* (see Table 2).

Table 2. *Haemoglobin content and number of erythrocytes in the blood of* A. s. mosquensis *Ogn. from the plains* (*Moscow region*) *and* A. s. ciscaucasicus *Ogn. from the Caucasus mountains* (*height* 1500–1800 m.)

	Haemoglobin content (according to Sahli)		No. of erythrocytes per mm.³ of blood	
Subspecies	No. of mice	Mean	No. of mice	Mean
A. s. mosquensis	23	104·3 ±1·76	43	9,118,796 ±156,313
A. s. ciscaucasicus	26	108·8 ±1·89	41	9,539,170 ±135,539
A. s. ciscaucasicus: % in relation to plain mice	26	104·3	41	104·6

A distinct difference in blood composition of mountain *A. s. ciscaucasicus* and plain *A. s. mosquensis* can be shown not only by the mean values, but likewise by observing the frequency distribution of individual values. But this difference is less pronounced than in plain and mountain mice belonging to one subspecies (see Table 1). The size of erythrocytes (πR^2) in both forms is almost the same, the mean for *A. s. mosquensis* being equal to $27{\cdot}13\mu^2$ (according to measurement of 1050 erythrocytes from 19 mice) and for mountain *A. s. ciscaucasicus*—$27{\cdot}35\mu^2$ (according to 1750 measurements of erythrocytes from 28 mice).

In this way, according to the physiological characters, the mice from the plains of the ante-Caucasus are nearer to the animals of the plains from the environs of Moscow, than to the *cisciscaucasicus* from the mountain regions; although the distance between the points where the animals of the plain and of the mountain were caught is several times less than the distance separating the place where the *ciscaucasicus* of the plain were taken from Moscow. Even more, the differences between the *ciscaucasicus* of the plain and of the mountain are somewhat more pronounced than between *ciscaucasicus* of the mountain and the *mosquensis* of the plain (see Tables 1 and 2). This intermediate position of the characters of *mosquensis* may be explained by the assumption that other climatic factors (in particular the temperature) in the northern regions may influence the physiological peculiarities of the mice belonging to this subspecies in the same direction as the conditions of life in the mountains.

4. Blood relationships of the mountain and plain forms

These results raise a new question. One might suppose, that the pronounced differences in blood constituents of mountain and plain *ciscaucasicus* are typical for these rodents and due to their belonging to different taxonomic forms and unconnected with the conditions of life in the plain and in the mountains. On the other hand the similarity established between the investigated physiological characters of the plain *ciscaucasicus* and *mosquensis* from the environs of Moscow may indicate that these different forms, by their morphological peculiarities, are more closely related taxonomically than mountain and plain *ciscaucasicus*.

In order to establish whether the Caucasian mountain mice constitute a special form, differing not only from those of the Moscow district, but also from those of the ante-Caucasian plains, approaching them by their morphological characters, Mrs Vera Avrech and I have made an investigation of the blood relationship of these three forms by means of the precipitation reaction. This method has been lately very much practised for the study of the blood relationship of different kinds of animals (see, for instance, Boyden, 1934; Hicks & Little, 1931).

In order to obtain specific antibodies, rabbits were immunized with the serum of the blood of wood-mice from the environs of Moscow (*A. s. mosquensis*). The serum of the blood of wood-mice from mountain and plain regions of the Northern Caucasus served as antigens for the reaction and was prepared in dilutions of from 1 : 100 to 1 : 25,000. Five series of experiments were made with 4–5 rabbits in each series. A complete description of these experiments is given elsewhere (Avrech & Kalabuchov, 1937). We determined the sensitivity of reaction by the end-point determination (antigen dilutions), and express the data taking Moscow mice as 100%. For the Caucasian mice from plains (Voroshilovsk and Nevinnomysskaja) we obtain similar results to those for the mountain mice from Utchkulan and Teberda (42·5–44·15 and 40·5–47·4).

From these data we conclude that the *ciscaucasicus* of the mountain and the plain belong to the same serological group and differ sharply from *mosquensis*.

In comparing these results with the preceding investigations we can state that the physiological distinctions between the mountain *ciscaucasicus* and those of the plain, established earlier, are not connected with the different relationship or origin of these forms. At the same time the similarity established between the investigated physiological characters of the plain *mosquensis* from the environs of Moscow and *ciscaucasicus* from the plain of the ante-Caucasus is not connected with their relationship or common origin. In other words, blood relationship of these three forms corresponds to their division into two subspecies according to morphological characters.

These data prove that the conditions of life in the mountains have such a strong influence on the physiological peculiarities of these rodents, that the mice of the mountains and of the plain belonging to the same form, by their blood relationship as well as by their morphological characters, differ sharply in their haemoglobin content and the number of erythrocytes. On the contrary, in two different subspecies of mice from the plains, *ciscaucasicus* and *mosquensis*, living in regions situated more than 1500 km. one from another, the blood composition as regards haemoglobin and red blood cells is alike. All these data enable us to affirm that the haemoglobin content and the number of erythrocytes in the blood of the mice are characters exclusively due to the conditions of existence of these rodents, and do not depend on the blood relationship or the origin of these forms.

5. Blood changes resulting from transfer of wood-mice to diferent levels

A transfer was made of the mountain *ciscaucasicus*, from a height of 1600 m., to the plain, and inversely a transfer of the forms of the plain of the same subspecies in an opposite direction—from the plain to the mountains (height 1475 m.).

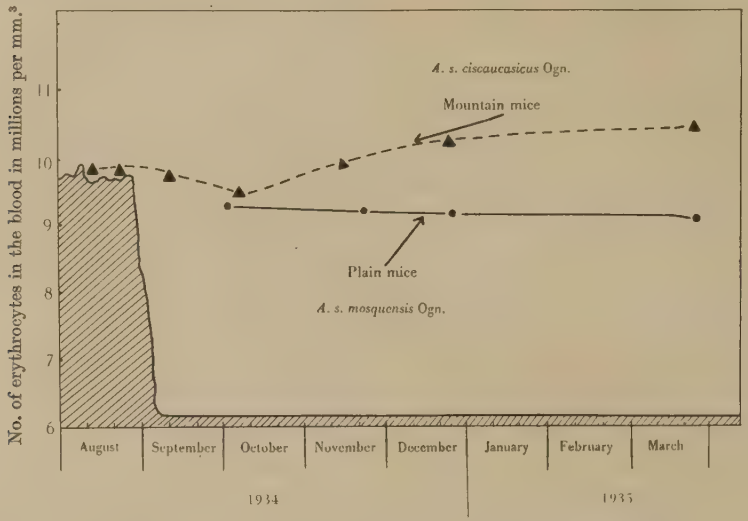

Fig. 2. Change in the number of erythrocytes in mountain *Apodemus sylvaticus ciscaucasicus* after transfer from the mountains to the plain.

Table 3. *Change in the number of erythrocytes of* 12 *specimens of mountain* A. s. ciscaucasicus *after transfer to the plain*

Place	Gondoray—Northern Caucasus height 1600 m.		Moscow—height 150 m.				
Time	15–14. viii. 34	17–27. viii. 34	8–14. ix. 34	1–15. x. 34	14–23. xi. 34	19–27. xii. 34	20–27. iii. 35
A. s. ciscaucasicus	9,851,777	9,898,833	9,726,600	9,585,000	9,976,340	10,265,450	10,673,333
Control: *A. mosquensis*	—	—	—	9,344,000	9,228,000	9,289,000	8,994,377

The data on the transfer of 12 specimens of mountain *ciscaucasicus* to the plain and on their remaining in these conditions during 7 months (2. ix. 34–26. iii. 35) are summarized in Table 3 and Fig. 3. In order to evaluate the influence of captivity on the changes in the composition of the blood, *mosquensis* of the plain from the environs of Moscow, kept under the same conditions, were periodically investigated at the same times.

The individual variation of these values in different specimens was quite insignificant.

We see that a transfer of the rodents under the conditions of the plain

produced at first only a decrease in the number of red blood cells, but later on, 2 months after the transfer the animals from the mountains, the number of erythrocytes again returned to its former level and even rose somewhat above it. At the same time, in the mice of the plain, kept under identical conditions, the number of erythrocytes remained on its former level or even fell somewhat below it. Similar results were obtained as regards haemoglobin content. The result of this experiment indicates the probability that the character we have studied in the *ciscaucasicus* of the mountains is a stable one in adult mice and does not alter with a change of height. Whether it is fixed hereditarily, or is a result of the development of young animals in conditions of a mountain climate, must be determined by further investigations.

The experiment of an inverse transfer has also yielded interesting results.

For this purpose 15 specimens of *ciscaucasicus* (from a height of 300 m. and investigated there between 1–9. vii. 35) were carried into the mountains on 10–13. vii. to a height of 1475 m. (Arkhys). The ascent to this altitude took 3 days (72 hr.).

After a sojourn of 2–3 days (15–17. vii.) in Arkhys we made a first investigation of the blood in some of the animals brought (8 specimens). A second investigation was made after a sojourn of 13–16 days in Arkhys (26–29. vii.). The remaining 7 mice were investigated only once, 25–26. vii., i.e. after remaining 12–13 days at a height of 1475 m., or after remaining 14–15 days at a height of more than 1000 m.[1]

The results obtained are given in Tables 4 and 6 and on Fig. 3.

Table 4. *Change in the number of erythrocytes in blood of the plain* A. s. ciscaucasicus *after transfer to mountains*

	Height 300 m. (Nevinnomysskaja)	Height 1475 m. above sea-level (Arkhys)			
		15–17. vii. 35		25–29. vii. 35	
No. of mice	1–9. vii. 35 per 1 mm.³	per 1 mm.³	% of initial value	per 1 mm.³	% of initial value
107	8,150,000	—	—	7,820,000	95·9
100	9,115,000	8,555,000	93·8	8,950,000	98·1
97	9,590,000	10,730,000	111·8	9,565,000	99·8
95	9,080,000	10,240,000	112·7	9,105,000	100·2
83	8,210,000	9,605,000	116·7	8,265,000	100·6
108	9,260,000	—	—	9,445,000	101·9
106	8,290,000	—	—	8,640,000	104·2
82	10,535,000	—	—	11,085,000	105·2
99	8,645,000	8,105,000	93·7	9,610,000	111·1
93	8,145,000	9,180,000	112·6	9,250,000	113·5
109	8,615,000	—	—	9,895,000	114·8
105	7,765,000	—	—	9,210,000	118·6
104	8,575,000	—	—	10,370,000	120·9
84	8,220,000	9,560,000	116·3	10,585,000	128·7
102	6,870,000	7,750,000	112·8	8,895,000	129·4
Mean	8,604,333	—	108·8	9,378,133	108·8

[1] Simultaneously we transferred to mountains 11 specimens of the field-mouse (*A. agrarius* Pall.) and one specimen of the yellow-necked mouse (*A. flavicollis* Melch.) caught and investigated between 25. vi. and 9. vii. in the environs of Nevinnomysskaja (see further).

According to these figures a sojourn of the mice at a height of 1475 m. for 3–4 days led already to an increase of almost 9·0 % in the number of erythrocytes as compared with the initial values. This increased number of erythrocytes remained the same after the rodents had been kept in the mountains from 13 to 16 days. We may notice that the increase of number of erythrocytes in blood of different specimens is not the same. In 3 mice out of 15 which were investigated a remarkable increase in the number of red blood cells only during the first days after transfer into the mountain (mice Nos. 97, 95 and 83–90, 15–17. vii) was observed; while at the end of the experiment these values were

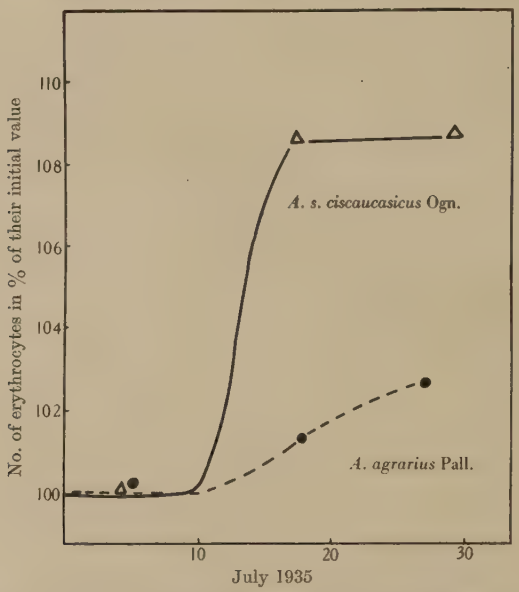

Fig. 3. Change in the number of erythrocytes in plain *Apodemus sylvaticus ciscaucasicus* after transfer from the plain to the mountains.

again practically the same as in the plain (99·8–100·6 % of initial value). In 2 mice (Nos. 100 and 107) the number of erythrocytes even fell to 95·9–98·1 % of initial value. But on the average the increase was quite pronounced.

Similar data were obtained for the haemoglobin content. The mean values for haemoglobin content rose in average from 102·5 % (after Sahli) to 109·1 %, or to 106·9 % of the initial value.

We see that whilst a transfer of adult mountain *ciscaucasicus* to the plain does not lead to a decrease of the haemoglobin content, and of the number of erythrocytes, a transfer of the animals to mountains calls forth a rapid adaptive reaction. *This difference apparently is connected with the peculiarity of*

reaction of animals to a change of external conditions depending on the direction of the changes in the external medium.

A change of conditions in a direction unfavourable to the organism (diminution of O_2 pressure) produces an adaptive reaction of the organism. The transfer of mountain animals to an atmosphere with high oxygen pressure does not produce any reaction.

Apparently this difference of reaction in the organism, when there is a change of external conditions and of their direction favourable for existence or else unfavourable, is a rather common occurrence. Thus, for instance, for a number of invertebrates there exists a certain degree of independence of intensity of their respiration upon partial oxygen pressure.

Termites, living under a poor oxygen supply, scarcely change the intensity of their respiratory metabolism in an atmosphere where the concentration of oxygen varies from 100 to 5% (Cook, 1932).

Data of the same kind have been obtained by Lindeman (1932) for the respiration of leeches. A change in the O_2 content in the water from 100 to 20% (taking the oxygen content in water at the beginning of the experiment as 100%) does not influence the intensity of respiration, which becomes lower only when the concentration of oxygen is below 20%. Hyman (1932), studying the gas exchange of *Nereis* in water poor in oxygen, and transferring the worms into the water saturated with O_2, found that the consumption of oxygen remained at the same low level even under new conditions. Recently Giaja & Gelineo (1936) have shown the same regularity for the respiratory exchange of rats. These mammals change their respiratory metabolism insignificantly when exposed to high oxygen content in air.

One can quote a whole number of examples of the same kind. Thus, for instance, if an animal passes into conditions of an abundance of food, this does not call forth any corresponding changes in the organism (i.e. which make the procuring of food more difficult): the animal simply loses less time in seeking necessary food. And inversely, a diminution in the quantity of food necessarily increases the intensity of the search for it and leads to a use of other kinds of food, etc. (see Elton, 1930).

There is no doubt that this type of reaction is characteristic for definite alterations of the medium, for definite processes and for definite species of animals. Thus, for example, Campbell (1926), placing rabbits in conditions of an increased oxygen content, obtained in them, in the course of 4 weeks, a decrease in the number of erythrocytes from 5·5 to 3 millions. It is true that this case is not to be compared with ours, as the rabbits were kept under conditions of excess of oxygen above the "normal". But the possibility is not excluded that for certain mountain forms the reaction will proceed in this direction. The research of Richter (1933) on lizards and Abderhalden *et al.* (1927) on marmots transported into the plain, suggests such a possibility.

6. The reaction of various species of plain rodents to decreased atmospheric pressure

Having established that *A. s. ciscaucasicus* from the ante-Caucasian plains possesses a capacity for rapidly and sharply increasing the haemoglobin content and the number of erythrocytes in the blood, with a diminution of atmospheric pressure, we carried out analogous experiments with wood-mice from other regions of the plains in the European part of the U.S.S.R.

The method differed from that used in the experiments described above, since the action of a decreased pressure has been studied in the conditions of pressure chambers. As such we used large glass jars of 32–40 l. capacity, with

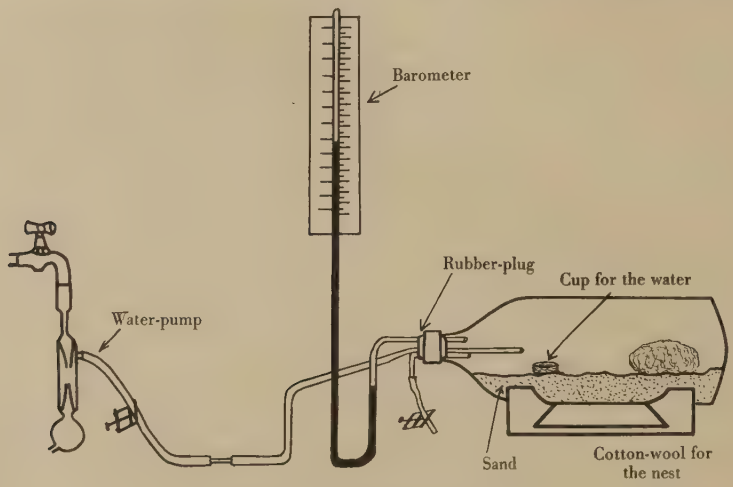

Fig. 4. Diagram of a pressure chamber for mice.

wide necks (diam. of opening 4–5 cm.). The opening of the pressure chamber was closed by a rubber stopper through which passed 3 glass tubes (see Fig. 4). One of the tubes was joined to a water-pump, another with a barometer and the third connected to the pressure chamber by a tube bearing an absorber of carbonic acid. Glass-wool was used as an absorber. It was periodically made damp by a solution of KOH through the tube. From the outside, all the tubes could be closed by means of screw clamps.

The pressure chamber was sanded with dry sand and on it were placed cotton-wool for the nest, and food (bread, carrots, wheat grains, sunflower seeds and nuts). Besides these, under the opening of the tube leading to the pump, a small cup for water was placed. Before introducing the animals, samples of the blood of the mice were investigated. The atmospheric pressure

was lowered gradually. At different moments the pressure in the pressure chamber corresponded to that at different heights above sea-level:

Beginning of the experiment	After 1 hr.	After 2 hr.	After 4 hr.	After 6 hr.	After 20 hr.	After 30 hr.
0–100 m.	500 m.	1000 m.	1500 m.	2000 m.	2500 m.	3000 m.

The pressure corresponding to a height of 3000 m. was maintained during the following 40 hr. or up to 70 hr. from the beginning of the experiment. Then the pressure was gradually increased (during 2 hr.) and after 72 hr. from the beginning the experiment was discontinued. The animals were taken out of the chambers and kept in cages for 1–2 hr. with plenty of food and water, their blood being repeatedly investigated.

During the experiment from 10 o'clock in the morning till 7 o'clock at night the pressure chamber was constantly ventilated. For this purpose the clamp on the tube leading to the absorber of CO_2 was opened so that with continuous working of the pump the pressure did not change. For the night the tubes with the glass-wool were filled with the alkali. In the same way the water in the cup was changed while the experiment went on. For this the pump was shut off and the tube leading to it was put into the vessel with the water. The water ran into the tube and in a few seconds the cup was refilled.

In Table 5 are given the data on the experiments with adult wood-mice of the plains from different regions of the European part of the U.S.S.R. (body wt. 17–26 g.).

Table 5. *Change in the number of erythrocytes in the blood of adult wood-mice* (A. sylvaticus) *after they had been kept in a pressure chamber for* 70 *hr.*

Subspecies and place	No. of erythrocytes per mm.³ At beginning	At end	%
(1) *A. s. mosquensis* from environs of Moscow	9,763,333	9,455,000	96·9
	6,740,000	6,780,000	100·6
	9,790,000	9,930,000	101·2
	9,300,000	9,630,000	103·5
	5,966,000	6,240,000	104·5
	7,870,000	8,262,500	105·0
	7,907,500	8,350,000	105·6
	1,004,000	11,336,000	111·0
	9,490,000	10,690,000	112·6
	9,652,000	11,800,600	122·5
	8,780,000	12,176,666	138·5
		Mean for Moscow mice	109·6
(2) *A. sylvaticus* subsp.? Asov-Black Sea region (Tarassovka and Tzymljanska)	8,430,000	9,733,333	114·4
	8,633,333	10,186,000	125·8

We see that these animals in the environs of Moscow and from the Asov-Black Sea region, like the animals of the Northern Caucasus (Table 4) increase sharply and rapidly the number of erythrocytes in the blood, when the atmospheric pressure becomes lower. Only single animals (2 out of 13) did not show it, and in one case a decrease in the number of red blood cells was ob-

served (96·9% of initial values). For the mice of the Moscow region the average increase in the number of erythrocytes was 9·6%. Thus the ability of increasing the number of erythrocytes owing to a lower pressure is characteristic not only of *A. s. ciscaucasicus* of the plain, but also for other wood-mice of the plain belonging to the other subspecies (*A. s. mosquensis* from the environs of Moscow and *A. sylvaticus* subsp.? from the Asov-Black Sea region).

In connexion with this the question arose, do other rodents of the plain possess the same capacity? We undertook therefore a series of experiments with 4 other mouse-like rodents:

(1) Field-mouse—*A. agrarius* Pall. from the environs of Nevinnomysskaja.

(2) Yellow-necked mouse—*A. flavicollis* Melch. from Crimea, Nevinnomysskaja and Leningrad.

(3) Red-backed or bank vole—*Clethrionomys* (=*Evotomys*) *glareolus* Schr. from the environs of Moscow.

(4) Grey hamster—*Cricetulus migratorius* Pall. from the environs of Berdjansk, South Ukraine.

The experiments on the action of a lower atmospheric pressure upon adult *Apodemus agrarius* (body wt. 18–35 g.) were carried out in the conditions of the pressure chamber as well as under natural conditions (see Table 6 and Fig. 4).

Table 6. *Change in the number of erythrocytes in the blood of adult field mice* (A. agrarius) *in the pressure chamber*

No. of erythrocytes per 1 mm.³ of the blood		
At beginning	At end	%
9,820,000	8,950,000	91·1
10,370,000	8,880,000	85·6
11,490,000	9,000,000	78·4
8,755,000	6,600,000	75·2
12,825,000	7,973,000	62·2
	Mean	78·5

These experiments in the pressure chamber showed that the field-mouse does not possess that ability to increase the number of red blood cells with a diminution of pressure, which has been found in *A. sylvaticus* (Tables 4 and 5). On the contrary, in a number of cases it shows a sharp diminution of these indicators leading to an average value of 78·5% of the initial value.

In experiments with a transfer of 15 specimens of *A. sylvaticus* and 11 of *A. agrarius* to the mountains in 1935, when these animals lived under conditions of lowered pressure for 10–16 days, in case of the field-mice we observed a very small increase of the number of erythrocytes—2·9% above the initial value (Fig. 3). In these experiments, the difference between the reaction of wood- and field-mice was also sharply pronounced (Fig. 3). In the same way in the pressure-chamber experiments, where two animals of these two different species were placed in one chamber, a sharp difference could be seen in the character of the reaction (Table 7). Finally it must be noted that in two cases the field-mice

perished even in the course of the experiments (a mouse in the pressure chamber and one in the mountains).

Table 7. *Comparison of the effect of a lowered pressure on adult wood- and field-mice in the same experiments.*

No. of exps.	*A. sylvaticus* No. of erythrocytes as % of the initial value	*A. agrarius* No. of erythrocytes as % of the initial value
30	125·0	85·6
27	111·2	78·4

Similarly, a diminished pressure in adult red-backed voles, *Clethrionomys glareolus* (body wt. 17–27 g.), produced a decrease in the number of erythrocytes (Table 8).

Table 8. *The change in the number of erythrocytes in the blood of adult red-backed voles* (Cl. glareolus) *after they had been kept in the pressure chamber for* 70 *hr.*

No. of erythrocytes at beginning of exp.	No. of erythrocytes at end of exp. Absolute value	%
10,900,000	10,260,000	94·5
10,610,000	10,316,000	97·0
10,326,000	10,115,000	98·0
9,103,000	7,775,000	85·3
6,403,000	5,676,000	88·5
10,935,000	8,470,000	77·5
	Mean	90·1

Grey hamsters (*Cricetulus migratorius*) also gave similar results (see Table 9) (body wt. of animals 25·4–31·8 g.).

Table 9. *Change in the number of erythrocytes in the blood of grey hamsters* (C. migratorius) *in the pressure chamber*

No. of erythrocytes At beginning	At end	%
9,476,666	7,999,666	84·4
7,910,000	7,270,000	92·1
8,746,666	7,883,333	90·3
8,556,000	7,800,000	91·3
8,146,666	7,650,000	93·9
	Mean	90·4

On the contrary, unlike these animals, a sharp increase in the number of erythrocytes has been observed in adult yellow-necked mice (*A. flavicollis*) (body wt. 26·1–36·3 g.) which, by their morphological characters and blood relationship (Avrech & Kalabuchov, 1937), are closely related to *A. sylvaticus* (Table 10).

The change of atmospheric pressure influences also the size of the erythrocytes, causing the young, larger cells to pass into the blood. We measured the size of erythrocytes on fixed smears. Fifty cells from every smear were measured before the beginning of the experiment and 50 after it was finished.

Table 10. *Change in the number of erythrocytes in the blood of yellow-necked mice* (A. flavicollis) *under influence of diminished pressure*

Conditions of exp.	Place of origin of mice	No. of erythrocytes: At beginning	At end	%
Pressure chamber	Environs of Leningrad	6,070,000	6,380,000	104·8
,,	Crimea	6,430,000	7,085,000	110·2
,,	,,	8,590,000	12,760,000	148·5
,,	,,	8,825,000	12,920,000	146·2
Transferred to the mountains	Environs of Nevinnomysskaja	7,795,000	9,850,000	126·2
			Mean	127·2

The averages of data obtained are given in Table 11. A calculation was made also of the change in the total surface of the erythrocytes, by multiplying the increase of their size (πr^2) in percentage by the indicator of change in numbers (also in percentage).

Table 11. *The change of red blood cell size and total erythrocyte surface (per unit of blood volume) under influence of diminished pressure*

Species and subspecies	Place of origin of rodents	Change (% of the initial value: mean for all rodents studied): πr^2 of 1 cell	No. of cells	Total surface of the cells
A. s. mosquensis Ogn.	Moscow	102·0	109·6	111·8
A. s. ciscaucasicus Ogn.	Nevinnomysskaja	104·6	108·8	113·8
A. flavicollis Melch.	Leningrad, Nevinnomysskaja, Crimea	100·8	127·2	128·2
A. agrarius Pall. (1935)	Nevinnomysskaja	98·0	102·9	100·8
A. agrarius Pall. (1936)	,,	103·8	78·5	81·5
Clethrionomys (=*Evotomys*) *glareolus* Schr.	Moscow	107·3	90·1	96·6
Cricetulus migratorius Pall.	Berdjansk	102·5	90·4	92·6

These calculations show that with a diminution of pressure, a sharp increase of the total surface of the erythrocytes is only observed in *Apodemus sylvaticus* (equal to 111·8–113·8% of initial value) and *A. flavicollis* (128%). In the field-mouse (*A. agrarius*) and the grey hamster (*Cricetulus migratorius*) no such reaction is seen, a decrease of the values in the pressure-chamber experiments being observed. In the red-backed vole (*Clethrionomys glareolus*) the decrease in the number of erythrocytes is compensated by an increase of their size, in consequence of which the total surface of the erythrocytes does not decrease so sharply.

At present we do not know the causes of these peculiar differences of reaction in the different species of rodents we have studied; they may be connected either with peculiarities of the blood-forming system, or with the existing reserve of already formed erythrocytes in the spleen and other organs (see Barcroft, 1934); but for us the very existence of these differences is the important fact. There is no doubt, that these peculiarities must have a strong influence on the state of the animals which find themselves in conditions of diminished atmospheric pressure. According to the researches of a number of

authors (for instance Barcroft, 1925; Grollman, 1930), an ascent into the mountains, at the beginning, produces a number of alterations of the normal breathing and blood circulation, connected with a compensation of an insufficiency of oxygen. The resulting increase of the haemoglobin content in the blood and of the number of erythrocytes, leads to a normal re-establishment of these disturbances in respiration and circulation (Grollman, 1930).

It is natural that a prolonged disturbance of the normal course of these processes in animals which do not possess the power of increasing the oxygen capacity of the blood, is harmful to the organism. We have already noted that, apparently in connexion with these peculiarities, two field-mice perished in a diminished atmospheric pressure, whilst the wood-mice, kept in the same conditions, remained alive in all the experiments. The changes in weight of the animals belonging to different species during the experiments are also quite remarkable (Table 12).

Table 12. *Changes in the body weight of rodents of different species under the action of a diminished pressure*

Species	Mean body wt. at end of exp. (% of the initial value)
A. sylvaticus (exps. in pressure chamber)	93·7
A. sylvaticus (exps. of transferring into mountains)	95·4
A. flavicollis	96·2
A. agrarius (exps. in pressure chamber)	89·0
A. agrarius (exps. of transferring into mountains)	77·1
Clethrionomys (=*Evotomys*) *glareolus*	89·5
Cricetulus migratorius	91·4

We see that *Apodemus sylvaticus* and *A. flavicollis* showed a small loss of weight (about 4–6%) whereas for three other species the loss of weight varied from 9 to 23%.

This indicates that the general state of the animals leaves no doubt as to the capacity of *A. sylvaticus* and *A. flavicollis* to adapt themselves more easily to a diminished atmospheric pressure than the three other species.

7. Summary and conclusions

The investigations that have been made are only a first step in the study of physiological differences of the plain and mountain wild rodents. First of all these experiments have enabled us to establish that the mountain wood-mice differ from the animals of the same species from the plains of the ante-Caucasus and the Moscow province by an increased quantity of haemoglobin and erythrocyte content, on an average of 6–12% (see Tables 1 and 2).

Next we have found that these peculiarities are not connected with the difference of origin of the animals from the mountain and from the plain; the study of the blood relationship as well as the morphological characters enable

us to include with certainty the ante-Caucasus mountain and plain mice into the same subspecies (*Apodemus sylvaticus ciscaucasicus* Ogn.).

That the differences in the haemoglobin content and in the number of erythrocytes do not depend either on the relationship or on the origin of different forms, is shown likewise by the data on the similarity of these indicators in the Caucasian mice of the plains and those of the Moscow province, which belong to two different subspecies by their morphological characters and blood relationship (Tables 1 and 2).

Thus, there is no doubt that these peculiarities are connected with the action of specific external conditions characteristic for the mountains, more particularly with the action of a diminished atmospheric pressure.

The experiments of a transfer into the mountains of *A. s. ciscaucasicus* from the plains, and the experiments in the pressure chambers with plain animals of these species from other regions, have shown that during several days an increase in the number of erythrocytes and the quantity of haemoglobin of 8–9% is observed (Tables 4 and 5 and Fig. 3).

In experiments of a transfer of the mountain animals into the plain and of keeping them in these conditions for several months (Table 3 and Fig. 2), it was seen that no diminution in the quantity of haemoglobin or in the number of erythrocytes takes place. Evidently this stability of the characters is connected with the circumstance that a higher pressure, i.e. a change in a direction favourable to the organism of the animals, does not cause any corresponding change in their blood.

It is possible either that the established physiological peculiarities of the mountain rodents are stable as a result of the development of the young animals in conditions of a lower pressure, or that they present already hereditary characters. An elucidation of this question may be possible after further investigation.

In studying the reaction of other species of rodents of the plain to a diminished pressure we have found that many of them are far from possessing the capacity of increasing the number of erythrocytes and their total surface with a diminished pressure (Tables 6, 7, 8, 9, 10, 11 and Fig. 3).

This is a peculiarity only of *A. sylvaticus* and *A. flavicollis*. The three other species (*A. agrarius*, *Clethrionomys* (=*Evotomys*) *glareolus* and *Cricetulus migratorius*) not only do not increase the number of erythrocytes and their surface in so prominent a manner as *Apodemus sylvaticus* and *A. flavicollis*, but in the majority of cases even show a decrease of these indicators.

In this way the proved lability of the given character for *A. sylvaticus* and *A. flavicollis* presents apparently a specific property of these animals.

The conclusion, that the lability of characters studied is connected with the other peculiarities on these two species, was confirmed also by the fact that we observed a similar reaction on diminished pressure in rodents from different plain points (for *A. sylvaticus*—environs of Moscow, Asov-Black Sea region,

environs of Nevinnomysskaja; for *A. flavicollis*—environs of Leningrad, Crimea and Nevinnomysskaja).

Finally, the fact that this ability of increasing these blood components is present only in these two nearly related species (see for instance data on blood relationship, Avrech & Kalabuchov, 1937) also confirms this conclusion.

Most likely this peculiarity determines the spreading of different species of rodents in the mountains. A comparison of the vertical distributions in the Caucasus of *A. sylvaticus* and *A. agrarius*, effectually shows that whilst the first species penetrates to a height of 1800–2000 m., the field-mouse reaches only a height of 600–700 m. (see Sviridenko, 1936). In the Semiretschje, according to the data of Schnitnikov (1936) the wood-mouse goes up into the mountains to a height of 3200–3300 m., the field-mouse only to a height of 1600 m.

Two other species, *Clethrionomys glareolus* and *Cricetulus migratorius* also do not go up into the mountains.

Certainly, in other cases, these physiological peculiarities may have no influence on the vertical distribution of the animals. Thus, for instance, *Apodemus flavicollis*, which possesses the same plasticity of the characters studied as *A. sylvaticus*, does not penetrate into the mountains as high up as this rodent (see Sviridenko, 1936), going up only to a height of 1000–1200 m. Apparently the distribution of this species is limited by its other ecological peculiarities. But this case does not refute the facts established as regards other species, especially as regards *A. sylvaticus* and *A. agrarius*, and it may be expected that the vertical distribution of a whole series of mammals can be limited by the peculiarities we seem to have established.

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ON A MARINE HOLOCENE FAUNA IN NORTH-WESTERN SCOTLAND

By D. F. W. BADEN-POWELL

1. The Udalain clay

The country mapped by the officers of the Geological Survey of Scotland on Sheet 71 includes a great many examples of raised beaches, and in the *Memoir* describing that country (Geology of Glenelg, Lochalsh and South-east Skye, 1910), the heights of the raised beaches are given as occurring up to about 100 ft. above the sea. The suggestion is also made (p. 168) that in the neighbourhood of Loch Alsh, a raised beach "varying in height from 30 to 40 ft. along the outer coast" seemed to rise in altitude when traced up Loch Alsh away from the open sea; the description continues—"At a point a few yards above the junction of the Udalain stream with the sea, Mr Clough and Dr Crampton found a deposit of shelly clay which probably represents the sublittoral zone of this beach."

This locality is important, because here one might expect to obtain evidence of the relation between the raised beaches and the later stages of glaciation, and the reported occurrence of a marine fauna at this point made further investigation the more desirable. As I was passing along the shores of Loch Alsh on my way to the Outer Hebrides in 1935, I decided to examine this shelly clay, and the results, which are set out in the present paper, are not in the least what I expected. It was not possible in the time available to prove the stratigraphical relation between the shelly clay and any particular raised beach, but the fauna of the clay is entirely "recent" in character, and as the depth of deposition represented is not more than 2 or 3 fathoms, it is almost certain that this clay is not contemporaneous with a high-level raised beach. This negative result is disappointing, but the fauna of this clay is worthy of description, especially for comparison with that described in this same *Survey Memoir* from Loch na Dal, in Skye.

I am extremely grateful to Dr W. A. Macfadyen for extracting and identifying the Foraminifera, and for his suggestions about the Foraminifera in the clay from Loch na Dal; I also wish to thank Dr F. W. Anderson for advice about the Loch na Dal fauna, and Mr J. R. le B. Tomlin for help in the identification of the Mollusca.

2. Fauna of Udalain and Loch na Dal

In the field, the shelly clay was found in a natural stream exposure on the left bank of the Allt Udalain, about 600 yd. downstream from Nostie Bridge, very near the point where the stream flows into Loch Alsh, about 1½ miles west

of Dornie Ferry. Only 2 ft. of the clay are exposed in the bank of the stream, capped by 6 in. of gravelly alluvium, but the clay continues under water, and in fact forms the bed of the stream. The height of the top of the clay was found (by hand-level) to be not more than 5 ft. above the highest point at which seaweed is now growing in the stream. Some larger shells were collected in the field, and samples of the clay were brought away, for washing out Foraminifera and smaller shells.

The clay at Loch na Dal in Skye was not visited by me, but the fauna from this locality as reported in the *Survey Memoir* is so similar to that found at Allt Udalain, that the two are conveniently described together, even though the Loch na Dal shells have not been available for direct comparison. The mode of occurrence of the Loch na Dal clay is thus described in the *Survey Memoir* (Anon. 1910, p. 165): "In the bed of Abhuinn Ceann-lochan (Loch na Dal), about 150 yd. above the foot of the burn, but only 25 to 40 yd. above the highest point to which ordinary spring tides ascend, a muddy shell-bed was observed which probably belongs to the neighbouring 20-feet beach, or else to some other below the 100-feet." The distance, measured in a direct line, between Loch na Dal and the mouth of the Allt Udalain is about 12 miles.

Foraminifera. The list of species from Udalain, and the comparison with the living fauna of the district and with the species found by the Survey at Loch na Dal, are taken from the report kindly supplied by Dr Macfadyen. The abbreviations used are: v.r. = very rare; r. = rare; f. = frequent; c. = common; a. = abundant.

List of Foraminifera from Allt Udalain

Spiroloculina nitida d'Orbigny	v.r.
Quinqueloculina angulata (Williamson)	v.r.
Q. fusca Brady	v.r.
Q. subrotunda (Montagu)	r.
Triloculina circularis Bornemann	r.
Trochammina squamata Jones & Parker	r.
Textularia gramen d'Orbigny	v.r.
Bulimina marginata d'Orbigny	r.
Buliminella elegantissima (d'Orbigny)	v.r.
Virgulina fusiformis (Williamson)	v.r.
Bolivina pseudoplicata Heron-Allen & Earland	f.
B. variabilis (Williamson)	f.
Lagena catenulata (Jeffreys M.S., Williamson)	r.
L. clavata d'Orbigny	v.r.
L. filicosta Reuss	v.r.
L. laevis (Montagu)	v.r.
L. lineata (Williamson)	v.r.
L. lucida (Williamson)	r.
L. marginata (Walker & Boys)	c.
L. perlucida (Montagu)	v.r.
L. protea Chaster	v.r.
L. scalariformis (Williamson)	v.r.
L. substriata (Williamson)	v.r.
L. trigono-marginata Parker & Jones	v.r.
L. williamsoni (Alcock)	f.
Guttulina lactea (Walker & Jacob)	v.r.
Uvigerina angulosa Williamson	v.r.
Globigerina bulloides d'Orbigny	v.r.
Patellina corrugata Williamson	f.

Discorbis mediterranensis (d'Orbigny) (Heron-Allen & Earland)	c.
D. praegeri (Heron-Allen & Earland)	v.r.
D. turbo (d'Orbigny) Brady	v.r.
Cibicides lobatulus (Walker & Jacob)	c.
Planorbulina mediterranensis d'Orbigny	r.
Acervulina inhaerens Schultze	v.r.
Rotalia beccarrii (Linné)	f.
R. perlucida Heron-Allen & Earland	v.r.
Nonion depressulus (Walker & Jacob)	f.
Elphidium crispum (Linné)	a.
E. excavatum (Terquem)	r.
E. incertum (Williamson)	v.r.
E. macellum (Fichtel & Moll)	r.
E. oceanense (d'Orbigny)	f.

Ostracoda were frequent, and Polyzoa occurred.

List of Foraminifera from Loch na Dal, Skye (Anon., 1910, pp. 192–3)

Revised nomenclature, on the assumption that the original identifications were correct.

(+ =recorded from Udalain; NR =not recorded from Udalain)

Memoir name	Revised name and remarks
Miliolina agglutinans (d'Orb.)	*Quinqueloculina agglutinans* d'Orb. NR. This may possibly be a wrong identification for *Q. fusca*
Textularia gramen d'Orb.	*Idem* +
Verneuilina polystropha (Reuss)	*V. scabra* (Williamson) NR
Bulimina marginata d'Orb.	*Idem* +
B. elegans d'Orb.	*Idem* NR
B. fusiformis	*Virgulina fusiformis* (Williamson) +
Bolivina punctata d'Orb.	*Idem* NR. This may possibly be the form I have identified as *B. variabilis* (Will.)
B. plicata d'Orb.	*B. pseudoplicata* Heron-Allen & Earland +
Lagena laevis (Montagu)	*Idem* +
L. semistriata Will.	*Idem* NR
L. squamosa (Montagu)	*Idem* NR, but probably the same as my *L. catenulata, scalariformis* or *hexagona*
L. globosa (Montagu)	*Idem* NR
L. lucida (Will.)	*Idem* +
L. williamsoni (Alcock)	*Idem* +
L. laevigata (Reuss)	*Idem* NR. Possibly included by me under *L. lucida*. I have not found it possible to separate it
L. costata Will.	*Idem* NR
Polymorphina compressa d'Orb.	? *Idem* NR } These may now be known under other (sub)
P. oblonga d'Orb.	? *Idem* NR } genera. My *Guttulina lactea* may be the
P. gibba d'Orb.	? *Idem* NR } same as one of these
Patellina corrugata Will.	*Idem* +
Planorbulina mediterranensis d'Orb.	*Idem* +
Truncatulina lobatula (W. & J.)	*Cibicides lobatulus* (W. & J.) +½
Rotalia beccarrii (Linné)	*Idem* +
R. nitida (Will.)	*Discorbis nitidus* (Will.) NR
Gypsina inhaerens (Schultze)	*Acervulina inhaerens* Schultze +
Nonionina depressula (W. & J.)	*Nonion depressulus* (W. & J.) +
Polystomella crispa (Linné)	*Elphidium crispum* (Linné) +
P. striato-punctata (F. & M.)	Definitely not this, which is a Red Sea species. Spp. recorded by me that would previously have been included as "striato-punctata" are *Elphidium excavatum, E. incertum* and *E. oceanense*

Forty-three species of Foraminifera are recorded here from the Holocene clay of Udalain: a shallow-water assemblage of recent forms, practically all of which are given by Heron-Allen & Earland as now living in the same area (Heron-

Allen & Earland, 1916, pp. 197–300 and Plates XXXIX–XLIII). The only form identified in the clay that is not certainly recorded by Heron-Allen & Earland is *Lagena protea* Chaster; the other small discrepancies may all be assigned to slight differences of nomenclature. No species derived from older rocks were recognized.

Compared with the fauna of 28 species listed from the clay of Loch na Dal (Anon., 1910, pp. 192–3). the Udalain clay has apparently 14 species missing. How far these may be due to different identifications or nomenclature it is impossible to say, but probably in several cases this would be found to be the explanation. Common species at Udalain not recorded at Loch na Dal are *L. marginata* and *Discorbis mediterranensis*.

As regards the climatic indication, the Udalain Foraminifera do not appear to show any difference from the present day conditions. The boreal species *Elphidium arcticum*, which might have been expected had the climate been appreciably colder, is not recorded.

With regard to salinity indication, there is nothing to suggest other than purely marine conditions. *E. crispum* is abundant, a species intolerant of brackish water. Of typical brackish water indicators, *Quinqueloculina fusca* is very rare, and *Trochammina inflata* and *T. macrescens* are not found.

Mollusca. The list of shells identified from the Udalain material is here combined in one table with the species and varieties recorded from Loch na Dal in the *Survey Memoir* (Anon., 1910, p. 192), so that direct comparison can be made. The original nomenclature used by Mr Thomas Scott in identifying the Loch na Dal shells is added where necessary. Of the 29 forms recorded from Loch na Dal, only 15 were recognized from Udalain, but the difference between the two lists may not point to a real difference of age, but rather to lack of exactly similar ecological factors at each place. As will be mentioned later, both deposits agree in the absence of such cold indicators as *Pecten islandicus* or *Astarte borealis*, both of which are common as Pleistocene fossils in the West of Scotland. The shells from Udalain are at the University Museum, Oxford.

	Udalain	Loch na Dal	Synonyms
Pecten maximus (Linné)	×	×	—
Mytilus edulis Linné	×	×	—
Modiolaria, cf. *discors* (L.)	×	—	—
Nucula, cf. *nucleus* (L.)	×	—	—
Axinus flexuosus (Montagu)	×	—	—
Lucina borealis (L.)	×	×	—
Lasaea rubra (Montagu)	×	—	—
Turtonia minuta (Fabr.)	×	×	*Cyamium minutum* (Fabr.)
Montacuta bidentata (Montagu)	—	×	—
Cardium edule L.	—	×	—
C. fasciatum Montagu	—	×	—
C. exiguum Gmelin	×	—	—
Dosinia lincta (Montagu)	—	×	*Venus lincta* (Pult.)
Venus striatula da Costa	×	—	—
Tapes pullastra (Montagu)	×	×	"Variety"
Tellina sp.	×	—	—
Abra alba (S. Wood)	×	—	—

	Udalain	Loch na Dal	Synonyms
?*Ensis siliqua* (L.)	×	—	—
Corbula gibba (Olivi)	×	—	—
Saxicava rugosa (L.)	—	×	—
?*Saxicavella jeffreysii* Winckworth	×	—	—
?*Poromya* sp.	×	—	—
Patella vulgata L.	—	×	—
Acmaea tessulata (Müller)	×	—	—
?*A. virginea* (Müll.)	×	—	—
Margarites helicinus (Fabr.)	×	—	—
Gibbula cineraria (L.)	×	×	*Trochus cinerarius* L.
Lacuna pallidula (da Costa)	×	—	—
L. vincta (Montagu)	×	×	*Lacuna divaricosta* (Fabr.)
Littorina littoralis (L.)	×	×	*L. obtusata* (L.)
L. saxatilis (Olivi)	×	—	—
?*L. aestuarii* Jeffreys	×	—	—
Littorina littorea (L.)	—	×	—
Onoba striata (Adams)	×	—	—
var. *aculeus* Gould	?	×	*Rissoa striata* (Adams) var. *aculeus* Stimps.
Alvania punctura (Montagu)	×	—	—
Rissoa parva (da Costa)	×	×	—
var. *interrupta* (Adams)	×	×	—
R. lilacina Récluz.	—	×	*Rissoa violacea* Desm.
R. albella Loven var. *sarsii* Loven	—	×	—
Skeneopsis planorbis (Fabr.)	×	×	*Skenea planorbis* (Fabr.)
Omalogyra atomus (Phil.)	×	×	*Homalogyra atomus* (Phil.)
Caecum glabrum (Montagu)	—	×	—
?*Turritella* sp.	×	—	—
?*Natica* sp.	×	—	—
Chrysallida obtusa (Brown)	—	×	*Odostomia interstincta* (Montagu)
var. *intermixta* (Scott)	—	×	?
Menestho divisa (Adams)	—	×	*Odostomia insculpta* (Montagu)
Odostomia minima Jeffreys	×	×	—
Bittium reticulatum (da Costa)	—	×	*Cerithium reticulatum* (da Costa)
Cerithiopsis metaxae (Chiaje)	×	—	—
Purpura lapillus L.	×	—	—
Neptunea antiqua (L.)	×	—	—
Buccinum undatum L.	×	—	—
Nassa sp.	—	×	—
Trivia europaea (Montagu)	×	—	—
Retusa retusa (Maton & Rackett)	×	—	—
Retusa subcylindrica (Brown)	—	×	*Utriculus umbilicatus* (Montagu)

Identification. The doubtful identifications in this list (indicated by a "?"), are mostly due to those specimens representing very young or broken shells. The specific names used are mostly in agreement with Winckworth's List (1932), but some departures have been made from it in the matter of generic names, such as *Lucina*, *Tapes* and *Purpura*, as these are so well known. In the attempt to bring the names used by Mr Thomas Scott in the *Survey Memoir* into conformity with those used for the Udalain shells, the only doubtful points are the use made by Mr Scott of "var." for *Tapes pullastra*, which is not further elucidated; and the variety *intermixta* of *Odostomia interstincta*. Mr Scott records (on p. 193 of the *Survey Memoir*) that this varietal name is used there for the first time, but gives it no definition.

Mode of occurrence. In the field, the clay at Allt Udalain gives the impression that *Lucina borealis*, *Cardium exiguum* and *Gibbula cineraria* are by far the commonest shells. Of the species in the faunal list, *Pecten maximus*, *Venus*

striatula and *Neptunea antiqua* were only doubtfully in situ; but the clay from inside the *Pecten* was washed for small shells, and yielded the same species as the main clay which was in situ. A sample of the main clay weighing about 1 lb. has been washed for small shells, both those which floated and those which remained at the bottom being collected. These shells contribute mostly to the number of species recorded. The following counts give an idea of the relative frequency of the more common species.

Lamellibranchs	No. of valves	Gastropods	No. of individuals
Turtonia minuta	89	*Onoba striata*	200
Cardium exiguum	30	*Skeneopsis planorbis*	137
Lucina borealis	19	*Rissoa interrupta*	49
Abra alba	11	*Omalogyra atomus*	26
Modiolaria, cf. *discors*	4	*Rissoa parva*	14
? *Saxicavella jeffreysii*	4	*Gibbula cineraria*	10
Axinus flexuosus	2	*Littorina littoralis*	4
Lasaea rubra	2		

Pecten maximus, *Cardium exiguum*, *Turtonia minuta*, *Axinus flexuosus* and *Lucina borealis* were all found with their two valves together. No adults of *Lacuna vincta* were found, but both this species and *Gibbula cineraria* were represented by a large number of young shells. The 10 individuals of *G. cineraria* mentioned above were adults.

Climate. The assemblage of Mollusca found in the Udalain clay does not appear to differ from the general fauna now found living in the Hebridean area. Certainly no definite indicators of either a colder or warmer climate are recorded. It will be noticed that the frequency of *Rissoa interrupta* is higher than that of *R. parva*, and in my description of the raised beach at Portland Bill (Baden-Powell, 1930, p. 72) I suggested that this might be an indication of colder conditions (see also Jeffreys, 1867, p. 25); but in the absence of more definite evidence than this, the ratio between these two forms must be treated with caution as an indicator of climate, because *R. interrupta* was more common than *R. parva* in a sample of Estuarine clay from Northern Ireland, a deposit which is otherwise known to have a warm climatic equivalent (Baden-Powell, 1937, p. 94).

It has been suggested in the past that favourable, if not actually warmer, conditions are represented by shells which are extra large in size. Brady *et al.* (1874, p. 81) record that *Pecten maximus* "of enormous size" was found near Colintraive, "in a shell-bed...exposed at low-tide which has been confounded with the true glacial clay, but which certainly belongs to a very different age". The actual size of the shells at that place is not given, but Lloyd Praeger (1893, p. 218) also mentions extra large shells of *P. maximus* in the Estuarine clays of Northern Ireland, giving the size as 6×7 in. The example from Udalain measures $4{\cdot}75 \times 5{\cdot}5$ in., which appears to be of normal size, Jeffreys giving as an average $4{\cdot}5 \times 5$ in. Certainly the *P. maximus* and the rest of the fauna from

Udalain are not stunted. They indicate growth under favourable conditions, but give no actual evidence of a warmer climate.

Salinity and depth of deposition

No brackish water forms were found in the Udalain clay, and the assemblage is typical of purely marine conditions. As regards depth of deposition, forms from both the tidal and the Laminarian zones are present, but those from the Laminarian zone are by far the most frequent. I do not believe that an accurate estimate of depth of deposition can be made by comparison with details of living depth-distribution. Praeger's method (1893, p. 214) is the most practical which has been suggested so far. This is "to select a number of its most abundant and characteristic shells, and note the minimum depths in which those species now live in local waters... by taking the average of these minima, a minimum depth is arrived at, which is in all likelihood pretty near the mark". If this method is applied to the Udalain shells, the minimum depth of deposition is about 2·5 fathoms (5 m.), and considering the fauna as a whole, a depth of from 2 to 3 fathoms seems fair. *This would indicate that the degree of submergence represented by the Udalain clay is from* 12 *to* 18 *ft., perhaps as much as* 25 *ft., if the slight altitude above present sea-level is taken into account.*

In the *Survey Memoir* (1910, p. 193), Mr Scott is wisely reticent about the precise depth of deposition represented by the Loch na Dal clay, but indicates that almost all the forms recorded by him now live in the littoral (tidal) or Laminarian zones, but that the occurrence of *Littorina* and *Cardium edule* indicate that this clay was not far removed from the tidal zone in depth. The fauna certainly indicates slightly shallower conditions than at Udalain, but from the description in the *Memoir* (1910, p. 165) the Loch na Dal clay may be at a slightly greater height (?10 ft. above high-water mark) than the Udalain clay at only 5 ft., so that an equal degree of submergence may well be represented at the two localities.

Comparison between the assemblage found fossil in the Udalain clay and the records of living Mollusca from this part of Scotland are instructive. According to Nicol's survey of the brackish water lochs on North Uist (1936, p. 176), *Onoba striata* (recorded by her as *Cingula semicostata*) and *Skeneopsis planorbis* were not found in a salinity of less than 20·4‰, and were more usually found in a salinity of 32·2–34·4‰. As these two Gastropods are by far the most common in the Udalain clay, this comparison supports the evidence derived from the assemblage of Foraminifera, that the salinity of the water in which the clay was deposited approaches that of the open sea.

Such comparisons also throw some light on the depth of deposition. Of the three most abundant Lamellibranchs in the Udalain clay, *Turtonia minuta* is known to be more common at low-water mark and in the Laminarian zone, than between tide marks (Jeffreys, 1863, p. 261); *Cardium exiguum* (replacing *C. edule*, which is characteristic of the tidal zone) is almost restricted to the

Laminarian zone; and *Lucina borealis* is most common from the lower part of the tidal zone, downwards (Stephen, 1930, pp. 527 and 528). These comparisons show that the Udalain clay was more likely to have been formed in the Laminarian than in the tidal zone.

At the same time, a lower limit of the depth of deposition is indicated by comparison with dredgings of the living fauna which have been made in Loch Alsh (H. C. and R. Winckworth, 1923, pp. 65–7), by the negative fact that the species which live commonly at depths below 7 fathoms (such as *Calliostoma clelandi* and *Trichotropis borealis*) do not occur as fossils in the Udalain clay. All these comparisons with more modern biological work present us with a clear idea of the ecological conditions under which the Udalain clay was formed, and confirm our estimate of deposition in 2 or 3 fathoms of water.

Correlation. Although the faunal assemblage is not identical in the clays at Allt Udalain and Loch na Dal, these two localities have the following characters in common:

(1) A fauna which differs little, if at all, from that at present living in the neighbourhood, and certainly lacking the cold indications found in so many of the marine clays of Western Scotland.

(2) Indication that the level of the sea was from about 12 to 15 ft. above its present level at the time at which they were laid down.

These two common characters, as shown by an analysis of the fauna, are sufficient to suggest strongly that the deposits at these two places are almost, if not exactly, contemporaneous. There is no other deposit in the north-west of Scotland known to me which can be correlated with these on faunal grounds, but there is a low-level raised beach on the Island of Lewis which may possibly be contemporaneous with the Udalain clay. In 1933 and 1935 Mr Charles Elton and I visited the Outer Hebrides, and proved that there is a raised beach on the west coast of Lewis, near Galson Farm, about 7 miles south-west of the Butt of Lewis, and that it is older than a kitchen-midden, dated by Dr Graham Callander as belonging to the Iron Age (paper in the Press). No satisfactory fauna was found in this raised beach, but it ranged in height from 10 to 25 ft. above existing high-water mark.

In suggesting that this raised beach in Lewis may be contemporaneous with the Holocene clay at Allt Udalain and Loch na Dal, one is admittedly influenced by the fact that a similar degree of submergence is proved. Unfortunately, no evidence was found in the field of the relation of the Udalain clay to any archaeological horizon.

3. The Holocene age of the Udalain clay

The fossiliferous clays at Udalain and at Loch na Dal have been deliberately called Holocene in the present paper, in an attempt to escape from such vague expressions as "post-glacial", or the even more ambiguous "25-ft. raised

beach". The essential characters of the fossil assemblage in these clays, at least in the north-west of Scotland, are as follows:

(1) No extinct species are included, and they therefore agree with Lyell's Holocene as opposed to Pleistocene.

(2) The fauna indicates climatic conditions very like those of to-day, at least in this part of Scotland.

(3) The facies represents deposition in shallow water, even when found between present tide-marks, indicating a submergence which probably did not exceed 25 ft. as an absolute maximum.

It is always theoretically possible that some or all of these characters might be found combined in a deposit which can be proved stratigraphically to be Pleistocene (e.g. by its relation to the boulder clays). In such a case, we would be relying on relation to the glacial deposits as our criterion of age, which would mean that the faunal character of the deposit can no longer be used alone for dating purposes. But such a case is hypothetical, and in practice I know of no interglacial deposit in Western Scotland in which the three conditions are combined.

I suggest, therefore, that on empirical grounds these three conditions are characteristic of the Holocene of the west of Scotland. Examples should now be given of the Pleistocene deposits of Scotland, to show that this claim is well founded, but this is impossible within the length of the present paper. In a future paper (now in preparation) it will be shown that the glacial and interglacial marine deposits in Lewis contain Pleistocene shells which can be distinguished from the Holocene fauna at Udalain and Loch na Dal.

There is also some evidence that the difference between the Holocene and Pleistocene fauna is not only one of facies and climate. Three species of Mollusca are found in the clay at Allt Udalain, namely, *Acmaea tessulata*, *Littorina aestuarii*, and *Odostomia minima*, never appear to have been recorded from any British Pleistocene deposit, and if their absence from the Pleistocene of these islands is proved by future work, we must assume that they made their first appearance here in the Holocene, as they are also, apparently, unknown in the British Pliocene. It would seem that the famous "Estuarine Clays" of Northern Ireland would be classified as Holocene according to the definition of that term in the present paper, and it is significant that both *Littorina aestuarii* and *Odostomia minima* have been recorded from those deposits. Further, *O. minima* also occurs in the clay at Loch na Dal, which is here correlated with the Udalain clay. Whether these "first arrivals" are really significant, and whether further examples of a similar kind will be found, can only be shown by future work.

It was hoped as far as possible to restrict the subject of the present paper to the north-west of Scotland, but this seems a good opportunity for correcting a mistaken opinion of mine expressed in an early paper, to the effect that the

climatic indications of the "25-ft. raised beach" point to rather cold conditions (Baden-Powell, 1927, pp. 435–7). This mistake arose because the height of certain marine deposits was chosen as their essential medium for correlation, and it was believed that their fauna also supported this method, as a secondary consideration.

The actual beds considered were the Kinness Burn clay, in Eastern Fife, and the raised beaches and sea-floors at Torbay, Portland and March in Southern and Eastern England. If the faunal characters of these beds are given primary importance, those at Torbay, Portland and March are seen quite definitely to be of Pleistocene and not Holocene type, and this conclusion agrees with their stratigraphical relationship. This leaves only the clay at the Kinness Burn as indicating colder conditions than those of the present day, at a date in the Holocene. This evidence is based on statements in the Fife *Memoir* (1902, p. 304), and by certain earlier writers, that the cold indicator, *Macoma calcarea*, had been found in this clay. Prof. Innes, of St Andrews, has very kindly lent me some of the shells from this clay, and I am now inclined to assign them to very thin-shelled *M. balthica*, but this identification is by no means certain.

We can now see that in fact the evidence for cold conditions in the Holocene deposits depends on the identification of one species from the clay at the Kinness Burn. On the other hand, there is the suggestion of indication of warmer conditions, already mentioned, in the Monograph by Brady *et al.*, based on the size of *Pecten maximus*, and this is supported by an opinion expressed by Jamieson (1865, pp. 189 and 191), that the distribution of *Scrobicularia piperata* in the "Carse Clays" of Eastern Scotland, by comparison with its living distribution in the same area, indicates "a climate, if anything, milder than the present". If we add the whole weight of evidence of Praeger's classical work on the Holocene of Northern Ireland, we are forced to the conclusion that the Holocene marine beds of Scotland, when viewed as a whole, may have been laid down during a slightly warm period, like those of Northern Ireland.

This digression from the original subject of the present paper has been necessary in order to correct my mistaken opinion published in 1927. The essential thing to do is to correlate by faunal characteristics rather than by apparent similarities of height alone: then, where possible, the amount of submergence at any locality can be estimated, but always with reference to a bed which possesses a definite ecological assemblage.

4. Summary

Samples from a clay deposit several feet above high-tide level at Allt Udalain, on Loch Alsh, West Scotland, contained 43 species of Foraminifera and 41 species of Mollusca. The faunal association is similar to that of the present day, is marine, and probably lived at a depth of 2–3 fathoms. It

closely resembles that of another deposit in Skye, and is thought to be Holocene rather than Pleistocene.

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A NOTE ON THE DISTRIBUTION OF THE TWO SHREWS FOUND IN JERSEY

By T. C. S. MORRISON-SCOTT

Department of Zoology, British Museum (Natural History)

The contents of three lots of pellets of barn owl (*Tyto alba*) from three different localities in Jersey sent by Mr H. J. Baal of the Société Jersiaise for analysis are of interest with respect to the shrews.

So far as can be ascertained there are only two shrews in Jersey: *Sorex araneus fretalis* Miller[1] which differs from *S. araneus castaneus* Jenyns (the common shrew of Great Britain) in having the rostral portion of the skull relatively shorter, broader and deeper and in tending to have a lighter coloured pelage; and *Crocidura russula* (Hermann), the white-toothed or musk shrew, which occurs on the Continent and in Guernsey, Alderney and Sark but not in Great Britain, though a special form, *C. cassiteridum* Hinton, is found in the Scillies.

The following table gives the numbers of each shrew found in the pellets from the three localities:

	Date	*Sorex*	*Crocidura*	Total (all species of animals) in set
Longueville (inland)	24. ii. 37	32	0 (=0%)	120
St Martins (near coast)	13. xii. 36	41	3 (=7·3%)	141
Ile au Guerdain (islet off coast)	18. i. 37	14	8 (=57·1%)	52

It appears from this table that *Crocidura* in Jersey lives on the shores but not inland. (It has a uniform distribution in France.) Though more material is clearly needed to prove this theory, interesting support is forthcoming from *Cæsarea*, a work by Jean Poingdestre on Jersey, written in 1682, to which my attention was drawn by Mr Baal. Here the author says in Chap. 15 ("Of Things Detrimentall"):

> The 3d sort [i.e. of "field-mouse"] is not halfe soe bigg as any of the former sorts, being scarce worthy of that name, though the Latins call it Mus-araneus.... This word Mus-araneus is compos'd of a mouse & a spider; not that it participates of ye shape of ye spider, but of his poisonous quality.[2] Wee haue in Jersey an infinite store of them euery where, but those which heretofore were taken notice of as a rare Singularity proper to vs were those onely found neere ye sea upon Beaches among ye pebles, whose excrement is perfect muske,... as if one should say a Musk-mouse,....But those in inland parts of the Countrey were neuer, that I knowe, taken notice of to have the same Propriety, but were esteemed a differing kind & were not called Musquines, but Besaraignes or Musaraignes, for distinction.

[1] **Miller, G. S.** (1909). Ann. Mag. Nat. Hist. 3: 416.

[2] In many parts of the British Isles shrews are still believed to cause sickness and death in various animals, e.g. cattle.

It is interesting to find owl-pellet analyses confirming this ecological note of over 250 years ago.

The following are the complete analyses of the three lots of pellets:

	Longueville	St Martins	Ile au Guerdain
Talpa europaea L.	3	6	0
Sorex araneus fretalis Mill.	32	41	14
Crocidura russula (Hermann)	0	3	8
Clethrionomys caesarius (Mill.)	23	41	11
Mus musculus L.	0	3	0
Rattus norvegicus (Erxleben)	1	2	0
Apodemus s. sylvaticus (L.)	25	36	17
Bat (unidentifiable)	0	1	0
Passer domesticus (L.)	33	8	2
Turdus sp.	3	0	0
	120	141	52

It will be seen that there is a complete absence of *Neomys*, *Microtus* and *Arvicola*, none of which have yet been recorded from the island, though there is a *Microtus* (*M. sarnius* Miller) in Guernsey.

THE DISTRIBUTION OF THE GREY SQUIRREL (*SCIURUS CAROLINENSIS*) IN GREAT BRITAIN IN 1937

By B. T. PARSONS and A. D. MIDDLETON

From the Bureau of Animal Population, Oxford University

(*With* 1 *Figure in the Text*)

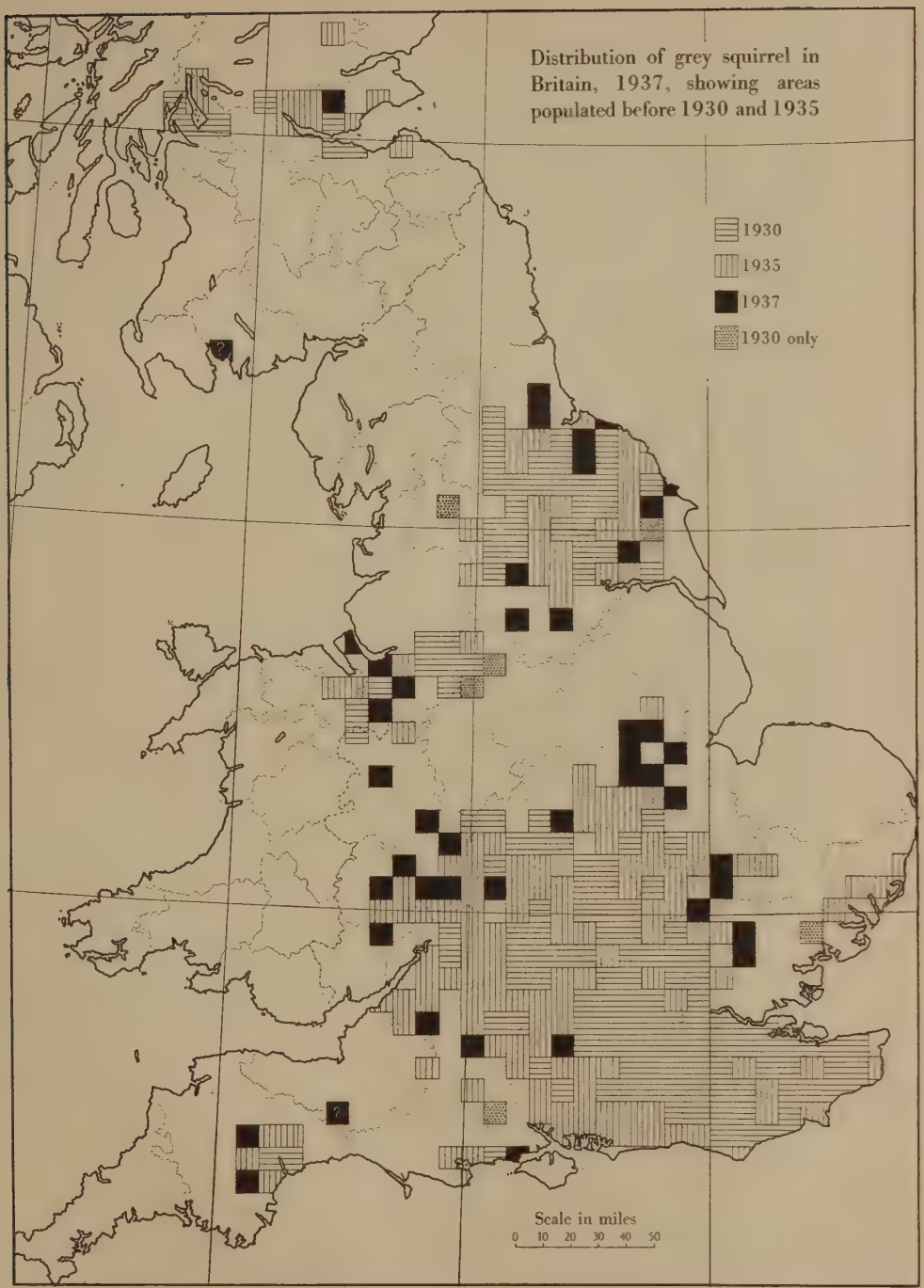
1. Introduction

During 1936–37 attempts were made to obtain records of the further spread of the grey squirrel since the last investigation (Middleton, 1935). We were concerned not so much with confirming previous observations as with finding new localities around the edges of the 1935 areas.

Information was sought by letters in the press, particularly in the local county papers, and by broadcast enquiries through the courtesy of the British Broadcasting Corporation. Once again we are indebted to the Automobile Association, whose road patrols were able to report many new localities; and also to the Chief Constable of Devon, who kindly obtained data on the squirrels around Exeter from the officers of the Devon Constabulary. We wish to thank Mrs Helen Chitty for much help in the mapping.

The number of records received is shown below, and it will be seen that 968 reports were sent in from 30 counties of England, from Wales, and from 9 counties of Scotland. In some cases, e.g. Bournemouth Gardens, many similar reports were received for the same locality, and, while each is counted in the table, only one is used on the map. The detailed correspondence, records and maps are filed in the Bureau of Animal Population.

Bedfordshire	7	Middlesex	22
Berkshire	45	Monmouthshire	1
Buckinghamshire	20	Northamptonshire	12
Cambridgeshire	3	Oxfordshire	27
Cheshire	51	Rutland	2
Devon	18	Shropshire	2
Durham	8	Somersetshire	2
Essex	6	Surrey	169
Gloucestershire	38	Sussex	54
Hampshire	52	Warwickshire	21
Herefordshire	5	Wiltshire	7
Hertfordshire	47	Worcestershire	11
Huntingdonshire	3	Yorkshire	153
Kent	84		
Leicestershire	5	Wales	6
Lincolnshire	6	Scotland	45
London	36	Total	968


Distribution of grey squirrel in Britain, 1937, showing areas populated before 1930 and 1935
1930
1935
1937
1930 only
?
?
Scale in miles
0 10 20 30 40 50

After the map had been made on the same principle as that for the 1935 survey, it was decided to record the spread of the squirrels by means of a grid system. The advantage of this system is that it equalizes areas where there are few and many observers: for a square containing one record counts as much as one containing many. Drawing a grid on the map also does away with arbitrary contour lines round the outside points, and it enables the area of distribution to be estimated.

For our purpose the grid was one of $\frac{1}{2}$ in. squares (scale of map 16 miles to 1 in.), giving areas of 64 sq. miles each. As the map was on a conical projection, 0^{c} longitude was taken as the vertical guide line and Greenwich as the starting point. Parallel lines $\frac{1}{2}$ in. apart and at right angles to the meridian were drawn, and it was then easy to complete the system of squares.

By means of this grid the areas from which we had reports of occupation in 1930, 1935 and 1937 were transferred from their respective maps. For 1935 and 1937 the original maps were used, while for 1930 a map was redrawn from Middleton's paper of that date (Pls. 3–5).

2. Present distribution

There are six main areas in Britain occupied by grey squirrels:

(1) Central area: including the whole of the south-eastern counties and south midlands, northwards to Leicestershire and Lincolnshire, westwards to Herefordshire and Wiltshire.

(2) Bournemouth district: still mainly confined to the coastal strip from Poole to Southampton.

(3) Devonshire: arising from separate introduction at Exeter, has spread into surrounding country.

(4) Cheshire and North Wales: arising from introductions into Denbighshire and Cheshire, now combined into one area.

(5) Yorkshire: covers a large part of all three Ridings and extends over the Tees into Durham.

(6) Scotland: from centres in Dumbartonshire, Dunfermline and Edinburgh gives rise to rather sporadic distribution in several areas.

The following table gives the number of occupied squares on the grid map for 1930, 1935 and 1937 together with a calculation of the total area occupied at the time of each survey.

	Central	Bournemouth	Devon	Cheshire	Yorkshire	Scotland	Isolated records	Total area (sq. miles)
1930	100	1	2	11	31	8	2	9,920
1935	201	4	6	14	43	18	6	18,688
1937	225	5	8	18	53	19	2	21,120

The area figures are probably too high as, on the marginal zone, a single record falling within a square on the grid attains a significance of 64 square miles of

occupied territory. The areas given should, therefore, be regarded as the total range of the squirrels rather than the area completely populated by them.

The stippled squares represent areas from which reports were received in 1930 but where no squirrels have been recorded since: these may have been killed out or at any rate have not increased to a noticeable extent. The five squares apparently due to sporadic appearances during 1935 in Suffolk are of interest: no further reports have been received from this county. The few blank squares within the main areas are probably occupied but, by chance, no records happen to occur within those squares.

The 1935 vertical hatched area shows a great increase over 1930, especially in the Central, Bournemouth and Devon areas.

Extension of range in the central area since 1935 has amounted to 24 squares, mainly in the marginal zone from Lincolnshire to Monmouth. The occurrence of the animal at Shrewsbury and at Newton Court, Monmouth, is of interest; while it is also found now on the Somerset side of the Avon near Bristol. In the latter county it has also been reported from near Taunton, but confirmation of this is desirable. Some increase has taken place near Exeter: here, as in the central area the spread is mainly westward, having now reached Ashburton. In the Bournemouth district there is little change, though the squirrels are now stated to be numerous at Parkstone.

In Yorkshire, as in Essex, there has been less movement of the squirrels; but in time we may expect squirrels from this area to link up with those in the central and Cheshire areas. The whole of North Yorkshire, with Darlington and South Durham, most of West Yorkshire, as far as the Pennines, and parts of East Yorkshire are now occupied. In the Cheshire and North Wales district extension northwards has occurred to near Mold and also into the Wirral.

Little change is observed in Scotland apart from a slight spread on the east. A squirrel reported in Kirkcudbrightshire is far from any previous record and requires confirmation, though it may be descended from those introduced into Ayrshire; Middleton (1930), however, could find no traces of these squirrels.

3. Numbers

In a previous paper (Middleton, 1935) figures of the numbers of squirrels killed on four different estates were given. It is now possible to bring some of these up to date, as follows (figures are for the years ending 30 April):

Year	Burnham, Bucks (500 acres)	Wychwood, Oxon (1400 acres)	Alton, Hants	Garrowby, Yorks
1932–33	290	450	200	190
1933–34	340	1059	170	301
1934–35	295	1427	225	227
1935–36	?	1125	(500)	364
1936–37	310	936		429

4. Summary

A survey has been made of the distribution during 1937 of the grey squirrel in Britain. The results are mapped on a grid system comparing the areas occupied in 1930, 1935 and 1937. The range of the grey squirrel continues to increase.

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A CONTRIBUTION TO THE ECOLOGY OF A GRASSLAND COMMUNITY ON GUADALCANAL ISLAND, BRITISH SOLOMON ISLANDS PROTECTORATE

By R. J. A. W. LEVER

(*With Plate* 8 *and* 4 *Figures in the Text*)

1. Topography and climate

The island of Guadalcanal (Figs. 1 and 2) forms one of the southern chain of the Solomon Islands archipelago, and lies between 9° 15′ and 10° S. latitude and

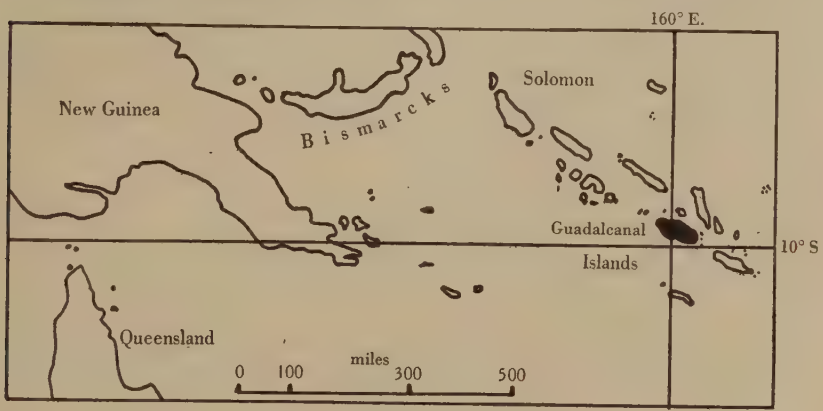

Fig. 1. Map of Western Melanesia.

159° 30′ and 160° 45′ E. longitude. It has an approximate area of 2500 sq. miles, somewhat smaller than that of the West Riding of Yorkshire; the highest mountain is 8000 ft. and is jungle-clad almost to the summit.

The author has from time to time taken meteorological readings and made collections in a habitat-zone near the northern coast in the vicinity of Lunga; the area is a grass plain, not found elsewhere in the Solomon Islands, which are otherwise covered with dense forests. The rainfall at Tenaru on the coast (about 1¼ miles away) has averaged 76 in. for the last 25 years, with a maximum and minimum of 133·5 and 43·5 in. respectively. These readings have been taken by a constant succession of managers of an adjacent coconut plantation, and the decimals can be regarded as not significant. Fig. 3 is a hythergraph, and is

made by plotting the mean temperature of each month as an ordinate against the mean daily rainfall of each month as an abscissa, and joining the points

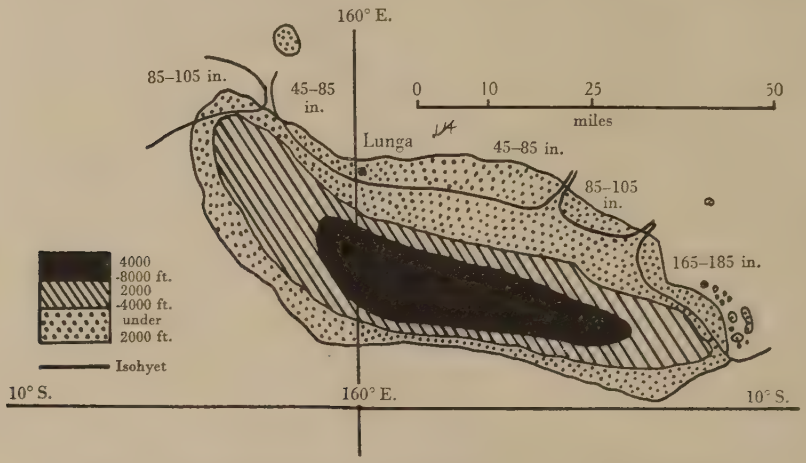

Fig. 2. Map of Guadalcanal Island, showing heights and rainfall contours (isohyets).

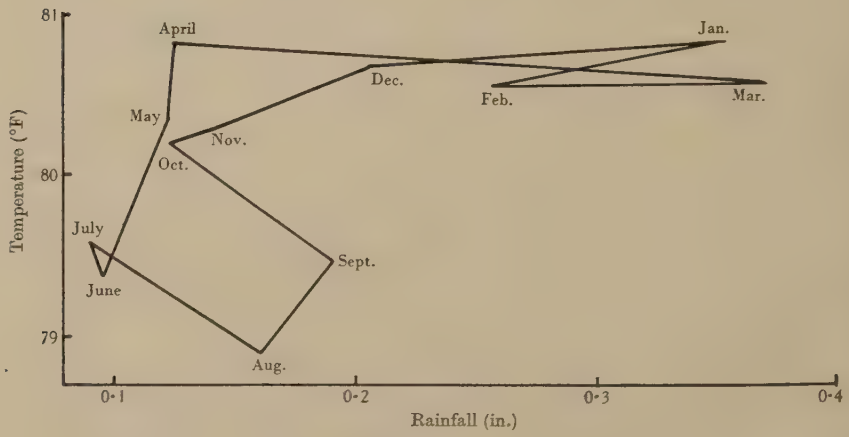

Fig. 3. Hythergraph, Tenaru, Guadalcanal.

thus obtained so as to make a closed figure. Some similarity is found to that worked out in the New Hebrides by Baker(**1**). The monthly values for one year at Lunga are given below:

1934–5	Average mean temp. ° F.	Average daily rainfall in in.
January	80·9 (hottest)	0·350
February	80·6	0·256
March	80·7	0·358 (wettest)
April	80·6	0·125
May	80·4	0·108
June	79·4	0·097
July	79·6	0·091 (driest)
August	78·9 (coolest)	0·165
September	79·5	0·199
October	80·2	0·120
November	80·3	0·142
December	80·7	0·207

2. The grass plain habitat

This area (Fig. 4) is characterized by two grasses, *Themeda australis* (kangaroo grass) and *Imperata cylindrica* (lalang), and consists of a flat stretch of ground with occasional ridges of raised coral which are covered with fairly dense jungle (Pl. 8). Owing to annual burning, the top soil is dark in colour on account of the carbonaceous matter which remains on the surface for a long time. The soil has been analysed in the Imperial Bureau of Soil Science at Rothamsted and is reported to be a dark brown loam with a hydrogen-ion reaction of 6·6, the amount of sand increasing with increasing depth.

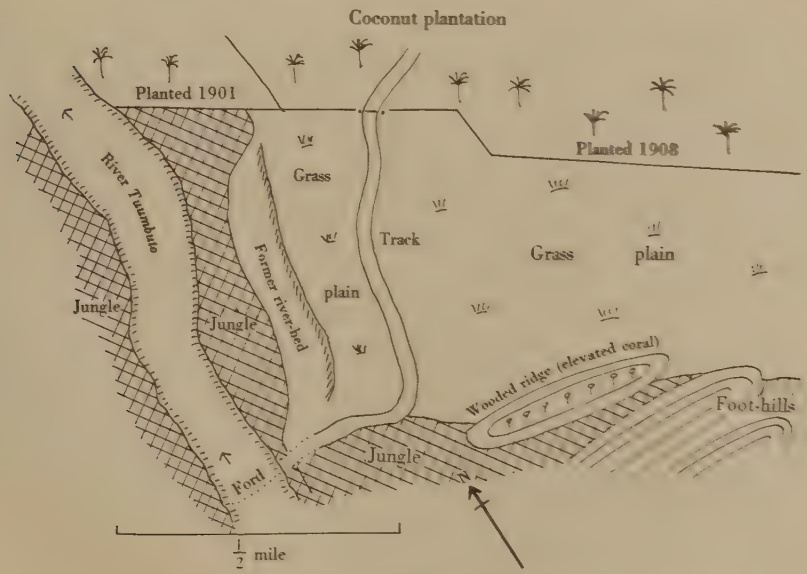

Fig. 4. Lunga, Guadalcanal Island. Plan of collecting area.

	Top soil	Subsoil at 3·5 ft. (%)
Physical analysis:		
Coarse sand (particles of 2·0–0·2 mm.)	4·6	6·0
Clay (particles of 0·002 mm. and below)	36·6	31·5
*p*H	6·5	6·7
Chemical analysis:	%	
Lime soluble in HCl	1·01	
Phosphoric acid soluble in HCl	0·17	
Available phosphoric acid	0·02	
,, potash	0·15	
,, soda	0·02	
Nitrogen	0·18	
Organic matter	11·44	

The amount of organic matter is high owing to free carbon from the burnt grass.

Maximum and minimum thermometers were placed at heights of 6–18 in. in clumps of the strong grasses, and gave maximum readings between 80 and 104°, and minimum readings of 55–76° F.; it is realized that radiation from the heated earth has occurred. Data (taken daily on the island of Tulagi, 20 miles to the north) show an average of 80·3% relative humidity. The amount of bright sunshine is recorded on a Campbell-Stokes recorder about 4 miles away, and shows a daily average of 6·2 hours.

Temperatures (in °F.)

June 1935			May–June 1936		
Max.	Min.	Day	Max.	Min.	Day
98	70	3	94	68	29–30
99	69	4	106	67	
104	70	5	95	72	30–1
101	70	7	105	71	
100	69		96	74	1–2
95	67		98	76	
100	70	7–8	80	66	2–3
104	69		83	55	
101	67		87	68	3–4
99	70	8–9	104	57	
99	72				
100	65				
100	68	9–10			
97	66				

3. The fauna

Determinations of the non-insect fauna have been made at the British Museum (Natural History); and of the insects alone at the Imperial Institute of Entomology, to whose Director, Sir Guy Marshall, C.M.G., F.R.S., the author is greatly indebted, as no progress can be made with such a survey till systematists have forwarded their determinations. The area in which the collections were made (Fig. 4) is approximately $\frac{1}{2}$ mile square and can be described as pure grassland with patches of such introduced herbs as *Sida* and *Mimosa pudica*.

Phot. 1. Grass plain with wooded foothills and mountains in background.

Phot. 2. Grass plain of *Themeda australis* and *Imperata cylindrica*.

MAMMALIA (1)

Sus papuensis (Less. & Garn.)	Wild pig

AVES (2)

Rhipidura leucophrys melaleuca (G. & G.)	Black and white fantail flycatcher. The commonest bird. Has *Degeeriella* and Dipterous parasites
Acrocephalus stentoreus (Hempr. & Ehrb.)	Warbler

REPTILIA (2)

Liolepisma noctua Lesson	Skink or lizard. Eats Isopod (see Crustacea)
Emoia cyanura (Lesson)	Skink. Larger of the two

INSECTA

ORTHOPTERA (14)

Austacris guttulosa illepida (Wlk.)	Largest Acridid
Heteropteris obscurella (Blch.)	Acridid. Red femora and tibiae
Gastrimargus marmoratus (Thnbg.)	Acridid. Explosive noise in flight
	Spotted wings
Oxya gavisa (Wlk.)	Acridid. Prey of *Tenodera* and spider A 2
Catanops angustifrons Wlk.	Acridid. Two black bars on hind tibiae
Locusta migratoria (L.) subsp.	Locust. Straw and green in colour
Tenodera costalis Blch.	Brown Mantid. Preys on *Oxya*. Parasitized by *Podagrion*
Gryllotalpa africana P.B.	Mole-cricket. On ground among grass roots
Gryllids O 12 and 13	Cricket
Tettigoniids O 6, 10, 11, 14	Long-horned grasshoppers

RHYNCHOTA (15)

Leptocorisa sp.	Slender brown bug
Lophops saccharicida Kirk.	Minute acute winged, orange bug
Sephena punctulosa Dist.	Plant hopper. Varies from white to green
Baeturia bicolorata Dist.	Cicada. Prey of fantail, *Rhipidura*
Parabolocratus arcuatus Motsch.	Red chevrons on wings
Agonoscelis rutila F.	
Curupira sp.	Red and yellow-green
Riptortus linearis F.	

Six species of Capsids, Reduvids, Jassids; and a horned Homopteron

LEPIDOPTERA (23)

Danais juventa Cram., *mangalia* Fruhst.	Marbled butterfly
D. mytilenae Feld., *decipiens* Butl.	Brown and white butterfly
Parnara mathias F.	Orange-brown skipper butterfly
Hypolimnas bolina L.	Butterfly: mimics *Danais*
Precis villida F.	Brown butterfly with eye spots
Euploea fraudulenta Butl.	Dark brown butterfly
E. eludens Butl. subsp.	Dark brown butterfly
Mocis trifasciata Steph.	Large brown Noctuid moth
Nodaria sp.	Medium sized brown Noctuid moth
Hyblaea puera Cram.	Speckled, brown Noctuid
Cataclysta sp.	Moth. Silver, dark wing margin
Lamprosema diemenalis Guen.	Yellow and brown moth
Crambus malacellus Dup.	White and grey moth.
Lygropia quaternalis Zell.	Moth. Cream, orange markings
Sphenarches caffer Zell.	Grey plume moth

Eight other species

COLEOPTERA (7)

Trigonops platessa Hebr.	Green weevil
Trigonops sp.	
Elaterid	Click-beetle
Galerucids 2 spp.	Leaf beetles
Mordellid	

One other species

ODONATA (4)

Diplacodes trivialis Ramb.	Clear-winged dragon-fly
Neurothemis terminata Ris.	Purple-red dragon-fly

Two other species

	HYMENOPTERA (18)
Bracon sp.	Braconid parasite. Small, black abdomen
Disophrys sp.	Braconid. Hyaline wings
Cremnops fulgidipennis Cam.	Braconid. Black and orange; dark wings
Cardiochiles sp.	Black Braconid. On grass tips
Camptolynx sp.	Ichneumonid. Orange body, clouded wings
Echthromorpha pallidilineata Cam.	Large orange Ichneumonid
Aximopsis sp.	Black Chalcid
Platyscelio sp.	Black and elongate Proctotrupid
Podagrion sp.	Torymid (Chalcidoidea). Parasitizes ootheca of *Tenodera*. Very long ovipositor
Sphex cognatus Sm. (?*Chlorion*)	Large grey wasp
?*Ropalidia* (?*Icaria*) sp.	Small yellow and brown
Polistes lepidus F.	Large bee
P. bernardii le Guill.	Medium sized bee
Megachile (2 spp.)	Black and orange bee, on leaf tips
Crocisa coeruleifrons Kirby	Blue and black bee
Nomia sp.	Black and orange banded bee
Pheidole oceanica Meyr.	Black ant, on ground
	DIPTERA (18)
Musca vicina Macq.	Grey house-fly. Settles on domestic stock
M. ventrosa Wied.	Orange abdomen. Settles on domestic stock
Argyroamoeba sp.	Bombylid. Settles on bare ground
Chrysosoma salomonis Par.	Metallic green fly
Dolichopodid	
Syritta indica Wied.	Orange and black Syrphid fly
Pipunculus sp.	Black fly, on *Imperata* (grass)
Sarcophaga orchidacea Böttch.	Grey blow-fly.
Elassogaster sp.	Green thorax, blue abdomen
Nine other species	
	MALLOPHAGA (1)
Degeeriella sp.	Bird-louse on plumage of flycatcher, *Rhipidura*
	ARACHNIDA (5)
Attid	Metallic spider. Very active
Spider A 2	Attacks *Oxya* (grasshopper) but prey may escape from web
Three other species	
	CRUSTACEA (1)
Isopod	Small grey woodlouse. Prey of lizard *Liolepisma*
	MOLLUSCA (1)
Gastropod	Small white snail, at foot of grasses

The total number of species recorded is over 112, and although so few have been determined it still seems desirable to publish this paper about a region which has, except for insects of the coconut palm (**2**), and more generally (**3**), apparently not been ecologically treated before. Chapman (**4**) indicates that detailed studies of the grass or herb substratum in grassland communities are needed. Elton (**5**) shows that the most frequent value for numbers of species lies between 60 and 140; this is for temperature climates, and does not cover full surveys of woodland. The writer wishes to thank Mr C. Elton of the Bureau of Animal Population, Oxford, for help in the preparation of this paper.

The collection is stored at the Imperial Institute of Entomology, London, S.W. 7.

4. Summary

An ecological survey was made of the fauna of a grass plain dominated by *Themeda australis* and *Imperata cylindrica*, on one of the southern Solomon Islands. The climate is tropical, with an average rainfall of about 76 in. and an average temperature of about 80° F. The variations are small. The fauna included 1 mammal, 2 birds, 2 lizards, 100 insects (mainly Orthoptera, Lepidoptera and Hymenoptera), 5 spiders, 1 snail, and 1 wood-louse. Over 100 species were collected. These have not all been finally determined, the collections being deposited in the Imperial Institute of Entomology.

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HOST-FINDING BY INSECT PARASITES. 1. OBSERVATIONS ON THE FINDING OF HOSTS BY *ALYSIA MANDUCATOR*, *MORMONIELLA VITRIPENNIS* AND *TRICHOGRAMMA EVANESCENS*

By J. LAING

(*Research Fellow of Newnham College*)

From the Zoological Laboratory, Cambridge

(*With* 5 *Figures in the Text*)

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1. Introduction

It might be claimed that all the movements of an animal from one place to another are for the finding of something. It is quite certain, at any rate, that many of the movements of animals can be considered as searching activities. This paper is concerned with one type of such activity—its purpose is to investigate the problem of how certain insect parasites find their hosts. The investigation deals chiefly with the Chalcid parasitoid *Trichogramma evanescens* Westwood; but in addition a brief study is made of certain aspects of the behaviour of the Braconid *Alysia manducator* Panzer and the Chalcid *Mormoniella vitripennis* Walker.

2. Analysis of the problem

Before proceeding to the details of the behaviour of these particular insects it is necessary to consider some features of the general problem of how animals find the things they need.

The objects sought by any animal are different at successive periods of its existence—food at one time, shelter, a mate, or a medium for oviposition at others. Which of these objects shall be sought at any particular time depends, clearly, upon the internal condition of the animal, for example, its state of hunger or the ripeness of its germ cells. In addition, the immediate behaviour of the animal is directly affected by external factors. Thus, a special combination of external and internal conditions may be necessary before any particular object is sought. For instance, not until its ovaries are mature and environmental conditions, such as light and temperature, are suitable does an insect parasitoid search for its host.

When finding conditions are right, the animal moves about until the sought object is perceived. That is, for finding, powers of movement and of perception are both necessary. This double nature of the finding process introduces a difficulty. Contact without recognition is possible if the sought object (e.g. a host) is encountered outside a particular type of environment. In this case, since the host is not recognized as such, it cannot be regarded as found. Recognition alone, however, is insufficient, because perception or recognition of the host may occur without automatic sequence, or even without the possibility, of contact. The host can be said to be found, therefore, only when the two factors, contact and recognition, are together satisfied.

As Salt (1935, p. 414) has pointed out, a parasite cannot find a host unless the two animals are coexistent in time and accessible to one another in space. An area in which a parasite and a possible host are geographically accessible to one another may be large and contain within it many and widely different types of ecological stations. Since it is not possible for an animal to exist in all kinds of environments, both the host and the parasite will be restricted in their distribution to a particular type of station. This may be highly specialized or it may be generalized, but it will be limited.

It follows that a parasite, *A*, may occur at any time in one of three situations relative to a host, *B*. (1) It may be outside the area of distribution of *B* and incapable of entering. (2) It may be outside the area of distribution of *B* and capable of entering. (3) It may be inside the area of distribution of *B*. In the first case, it is impossible that *A* should ever find *B*. In the second case, before *A* can find *B* it must first find and enter *B*'s area of distribution. Once within that area the problem becomes the same as in the third case, where *A* has to find *B* when both are within the same limited area.

All questions of host-finding may, therefore, be dealt with under the two headings: (*a*) How does the parasite find the area in which the host occurs?

(*b*) How does the parasite find the host when both are within the same limited area? These two questions are discussed in the following pages.

3. Finding the area in which the host occurs

The movements of a parasite that is outside the area of distribution of its host, must be either entirely random with respect to that area, or influenced by the environmental factors characteristic of it. Where the parasite is capable of entering the host-area the latter alternative implies an attractive influence of the environment. In the first place, therefore, the query "how does the parasite find the host-containing area?" must be answered in each particular case by determining whether the parasite does seek a type of environment, irrespective of the presence or absence of hosts in it. Salt (1935, p. 414) is of the opinion that there are cases in which this phenomenon does occur: "Now it is certain that some parasites, and probable that many more, are first attracted not to a particular host but to a certain type of environment." The present section of this paper provides proof for this statement from consideration of evidence in the literature, and from experiments on *Alysia* and *Mormoniella*.

(*a*) *Cases in the literature*

The literature does not appear to contain any formal demonstration that parasites are primarily attracted to an environment rather than to any hosts that may be in it; but it does provide circumstantial evidence. It is obvious, of course, that parasites of wood-boring larvae must first of all seek trees, possibly even special kinds of trees, before they can find a host; that parasites of burrowing insects (such as Scoliid parasites of Scarabaeid larvae) must seek them in soil; and that the Hymenopterous parasites of aquatic insects begin their host-finding activities by seeking and entering water. Indeed, when a parasite is found to attack several hosts of quite different kinds, but having in common their occurrence in a particular ecological situation, some such attraction of the environment can be taken to be indicated. Evidence of this kind is common in the literature.

Picard & Rabaud (1914, p. 267), discussing parasitism by Braconids, give it as their opinion that, "Il apparait que, dans certains cas tout au moins, l'attirance exercée par un végétal donné est d'une plus grande importance que l'Insecte dont se nourrira la larve...." They illustrate this statement by reference to three species of the genus *Bracon*: *B. scutellaris* Wesm. which parasitizes indifferently *Grapholitha strobilella*, *Hylesinus*, etc.—that is, insects of conifers; *Bracon colpophorus* Wesm. which attacks the weevils of leguminous plants; and *B. variator* Nees, which "est parasite de Diptères et de Coleoptères n'ayant d'autre point commun que de vivre dans les fleurs des Composées". Giard (Picard & Rabaud, 1914) obtained *B. variator* from capitula of ragwort, *Senecio jacobaea*, attacked by *Phorbia seneciella*; Picard & Rabaud obtained it from thistle-heads containing sometimes the Curculionid *Larinus* or the

Trypetids *Tephritis* and *Urophora*, and sometimes Microlepidoptera (*Myelois*, etc.); and they even saw it ovipositing in capitula which contained no larvae.

Howard (1924, p. 36) remarks that "there are certain elements in parasitism which connect the parasitism not so much with the host insect as it appears in the system of classification adopted by entomologists as it does with the method of life of the host insect". He cites as an illustration the fact that species of Eurytomidae and Torymidae are parasitic on sawflies, Coleoptera, Lepidoptera and Diptera inhabiting galls, and states that "the excitation to oviposition is not the morphological character of the host insect but the gall which it inhabits".

Cushman (1926*a*, p. 6; 1926*b*, p. 33) brings forward two records indicating the importance of the host environment. *Epiurus pterophori* Ashm., which normally parasitizes Lepidopterous and Coleopterous larvae living in weed stems, has been reared from larvae of a sawfly *Ametastegia glabrata* Fallen that had entered the weed stems for pupation. A species of *Sympiesis* typically parasitic on leaf-mining Lepidoptera, is recorded from leaf-mining larvae belonging to three other orders—Coleoptera, Diptera and Hymenoptera—and has even been reared from the eggs of the large sawfly *Cimbex americana* present in willow leaves. Cushman is of the opinion that "Many parasitic Hymenoptera, especially those whose hosts are concealed within the tissues of their food-plants, are in the habit of searching for their hosts in certain sorts of locations, the sort of location being of nearly if not quite as much importance as the systematic position of the host insect".

Gahan (1933, p. 4) states that many of the parasites of the Hessian fly attack several other kinds of larvae inhabiting wheat and other grain plants, while insects generally parasitic on other wheat-infesting larvae are at times reared from the Hessian fly. From his observations he concludes that: "Aside from the Eupelmids, most of the Chalcidoids seem to be guided by the character of the plant and the location of possible hosts in it, rather than by taxonomic relationship of the species attacked." Further, after remarking that the Hessian fly is occasionally attacked by species of the two genera *Centrodora* and *Tumidiscapus*, which commonly parasitize eggs of Orthoptera inserted in grass stems, he concludes "The occurrence of these Aphelinids as parasites of the fly, therefore, is probably attributable to the same instinct that seems to guide the oviposition of many of the other Chalcidoids—that of thrusting their eggs into any insect body which happens to be suitably located in the type of plant which they habitually frequent."

The point emphasized by these authors is that, in the parasite's choice of a host, the characters of its environment are of as much or of more importance than its systematic position. The point that is here drawn from their data is rather a corollary of this view, namely, that some members of four groups of parasites (parasites of larvae living in flower-heads, of gall-living insects, of leaf-miners and of the insects which infest grass stems), when they search for

hosts, appear to find first a particular type of environment, and then proceed to seek the hosts themselves.

There are, moreover, in the literature, cases of parasites which oviposit in situations frequented by their hosts and do not actually find the hosts themselves. The Tachinid *Gonia capitata* lays its eggs on grasses, where they are eaten by their host, the grass-eating *Porosagrotis orthogonia* (Strickland, 1923). The Cyrtid, *Pterodontia flavipes*, lays its eggs on trunks of trees, where they hatch into minute active larvae. These then seek their hosts, the spiders which live on the tree trunks (King, 1916). According to Richardson (1925) the Tachinid *Eupeleteria magnicornis* Zett. larviposits only on foliage where the host caterpillars have crawled; while Tothill (1922) observes that maggots of *Ernestia ampelus*, a parasite of the fall web-worm, are deposited on the food-plant of the host in the vicinity of its web.

Cases similar to these, both of the type in which the parasite finds only the ecological situation and of the type in which it goes so far as to find traces of the host in that situation, could be multiplied from the literature. They fail, however, as a formal proof that an environment is attractive to a parasite quite apart from the presence of hosts. That proof is supplied by the following experiments.

(*b*) *Experiments with* Alysia manducator

Alysia manducator (Hymenoptera, Braconidae) is a parasite of several kinds of larvae which live in decomposing carcasses; among them being maggots of the flies *Calliphora*, *Lucilia*, *Muscina*, *Hydrotaea*, *Phormia* and *Fannia* and larvae of the beetle *Creophilus maxillosus* (Myers, 1927). If, in the course of its flight, the parasite approaches a carcass, it is attracted by the smell and flies towards it. Once on the carrion, it walks over the surface, stabbing frequently with its ovipositor until a larva is encountered. These stabbing movements of the ovipositor are provoked both by a sufficient concentration of carrion smell, especially by contact with the surface from which the smell emanates, and also by the stimulus of movement under the surface on which the *Alysia* is walking.

That the first attraction for *Alysia* lies in the carrion itself and not in the larvae contained in it, is suggested by the fact that the parasite is found on meat on which the fly larvae are not hatched (Myers, 1927) and is conclusively demonstrated by the following experiments.

The reactions of *Alysia* were tested in a simple choice-apparatus, similar in principle to the apparatus used by Krijgsman (1930) for investigating the reactions of *Stomoxys*. It consisted of a glass cylinder 4·0 in. long and 2·6 in. in diameter, with one circular hole half-way down its length, and with a removable tin lid at each end (Fig. 1). Each lid was pierced by a central cork through which fitted a glass tube, 4·2 in. long and 0·6 in. in diameter. Since the cork and tube projected a short distance through the lid into the cylinder, paraffin wax was poured into the lid to make a smooth and level surface from the outer

cylinder to the mouth of the tube. The parasites were admitted into the large cylinder through the central hole, which was surrounded by a small sleeve of muslin.

In the performance of an experiment, a cork was inserted into the distal end of each side tube; one cork bearing material the attraction of which was to be tested, and the other quite clean. The number of times an entry was made by an *Alysia* into each tube from the median cylinder during a period of 20 min. was counted. In order to eliminate any unequal effect of external influences, the apparatus was turned horizontally through 180° after the first half of each experiment.

A series of four experiments was carried out using the same 17 *Alysia* females for each. In the first, the end of each side-tube was closed with a clean cork. In the second experiment, each cork was wrapped in damp muslin, and between the muslin and the cork of one tube was placed a living *Calliphora* larva which had been washed in water and kept between sheets of clean damp filter-paper for the previous 18 hours. In the third experiment, an unwashed

Fig. 1. Apparatus for investigating reactions of *Alysia* to smell of carrion.

arva, straight from carrion, was substituted for the washed larva. Between this experiment and the next the smell of carrion was blown from the cylinder and the tubes were cleaned. In the fourth experiment, a small piece of the meat from which the larvae had come was inserted between the cork and the muslin. The results of these experiments are shown in Table 1.

Table 1. *Reactions of* Alysia *in choice-apparatus*

Exp. (17 *Alysia* ♀♀ used in all cases)		No. of entries to side-tubes in 20 min.		Observations
1	Control Clean corks	2 to tube A (clean)	0 to tube B (clean)	*Alysia* did not make stabbing movements with ovipositor
2	Washed larva	3 to larva	1 from larva	Larva stabbed
3	Unwashed larva	9 to larva	2 from larva	Larva stabbed
4	Carrion	12 to carrion	5 from carrion	Meat stabbed

Since the *Alysia* was attracted to a larva when it was covered with carrion juice much more than when it was clean, and since it moved towards a small piece of carrion without larvae in it, the smell of the decomposing meat must have been the attraction for the parasite.

The meat used in the above experiment, however, had contained larvae and the attraction might have been due to substances formed in the meat as a result of larval activity. Two further experiments were performed, therefore, to determine whether the parasite was attracted to meat which had not been infected with maggots. In these experiments, cotton-wool plugs to the side-tubes were used instead of corks. In the controls, both plugs were clean and damp; in the meat experiments, one plug was rubbed in the meat. This latter was lean steak, minced, and kept in a jar with a cloth top of double thickness. In the first experiment, the meat was almost fresh and had very little smell; in the second experiment, 2 days after the first, the smell was much stronger. The results of these experiments are shown in Table 2.

Table 2. *Reactions of* Alysia *to uninfected meat*

Exp.	No. of entries to side tubes in 20 min.		Observations
1 Control			
(*a*) Clean cotton-wool	0 to tube A (clean)	2 to tube B (clean)	No stabbing movements
(*b*) One plug of cotton-wool rubbed in fresh meat	12 to meat	1 from meat	Stabbing movements observed
2 Control			
(*a*) Clean cotton-wool	0 to tube A (clean)	0 to tube B (clean)	No stabbing movements
(*b*) One plug of cotton-wool rubbed in 2-day-old meat	12 to meat	0 from meat	Stabbing movements observed

In both experiments the parasites were observed occasionally to stab the cotton-wool which had been rubbed over the meat, or the glass tube near the cotton-wool.

It is clear from these experiments that *Alysia* moves to meat whether or not it contains, or has ever contained, larvae; and that the smell of the meat alone is sufficient to stimulate the stabbing movements of the ovipositor, by means of which larvae, if present, might be located.

(*c*) *Experiments with* Mormoniella vitripennis *Walker*

The Chalcid *Mormoniella vitripennis* (=*Nasonia brevicornis* Ashm.) is a parasite of the pupae of carrion-feeding Diptera. The following experiments indicate that this insect, like *Alysia*, is primarily attracted by the carrion environment of the host. The experimental method was the same as that described above. Three experiments were performed, using the same meat, which had never been infected with maggots. The first experiment was done when the meat was quite fresh, the second was performed 5 days and the third 9 days later. The results are shown in Table 3.

From these experiments it is clear that *Mormoniella* is attracted to carrion even when there are not, and never have been, hosts in it.

Incidentally, it is to be noticed that the attraction of fresh meat to *Mormoniella* is only slight, whereas the attraction of 9 days old meat is very

Table 3. *Reactions of* Mormoniella *to uninfected meat*

No. of *Mormoniella* ♀♀	Exp.	No. of entries to side tubes in 20 min.	
1 67♀♀	Control	7 to A (clean)	10 to B (clean)
	Fresh meat	19 to meat	11 from meat
2 70♀♀	Control	13 to A (clean)	15 to B (clean)
	5 days meat	22 to meat	14 from meat
3 60♀♀	Control	1 to A (clean)	3 to B (clean)
	9 days meat	42 to meat	3 from meat

pronounced. In this respect *Mormoniella* differs from *Alysia*, which responds markedly to the smell of fresh meat. This difference in the behaviour of the two insects is of significance in that *Alysia* is a parasite of larvae, whereas *Mormoniella* does not attack its hosts until they have pupated.

(*d*) *Discussion*

The conclusion to be drawn, both from evidence provided by the literature and from the results of the above experiments, is that some parasites do first seek a particular environment, in which they afterwards proceed to seek their hosts. The analysis of the process by which the parasite finds its host into two parts—the finding of the environment and the finding of the host in that environment—is, therefore, not merely a convenient theoretical division, but corresponds to an actual difference in the behaviour of the parasite.

This habit of parasites of seeking first a particular type of situation may prove of considerable economic importance. It is clearly possible that the area in which the parasite seeks its host may, in some cases, be more restricted than the area of distribution of the host species. In such a case, since the parasite does not find those individuals of the host-species that are outside the environment in which it searches, a proportion of the host population is in each generation inaccessible to the parasite and so escapes parasitism. For instance, it seems likely that one of the reasons why *Cephus cinctus* became a serious pest when it transferred from prairie grasses to wheat, was that the *Microbracon* which attacked it in its native grasses did not find it in wheat. The importance, from the point of view of biological control, of the inability of a parasite to find a proportion of its host population, has been discussed by Thompson (1929).

The question of the precise method by which particular parasites find the host-containing environment is one which must be answered separately for each parasite, since some will walk and others fly, some see and others smell. It is to be noticed, however, that in general the senses and the nature of the movement used in finding the environment may be quite different from those used in finding the host. Nicholson (1933, p. 171) has pointed out that many predators use two modes of locomotion when hunting their prey, "one of which is used in a cursory random survey of the environment for aggregations of prey or suitable places in which prey might occur, while the other is used for a

slower and more detailed random survey of places in which prey are likely to occur". In *Alysia*, as we have seen, different senses and methods of locomotion are used to find the carrion and the maggots it contains. The carrion is found by the sense of smell and is approached in flight; the host larvae are found chiefly by means of the tactile sense employed while the parasite walks over the carrion, stabbing with its ovipositor.

Not only, then, do some parasites find environments first and hosts later, they may also use quite different senses for the perception of the two and make quite different movements to reach them. What those senses and movements are, however, will differ greatly with different parasites, and must be especially determined in each particular case.

4. Finding the host in the host-containing area

(*a*) *Introduction*

Having found an environment in which the host occurs, the parasite is next faced with the problem of finding the host itself. That problem is the subject of the present section of the paper.

In the investigation of this subject, only one experimental animal has been used, the Chalcid *Trichogramma evanescens* Westwood. This insect is very suitable for the problem, for it is so small ($\frac{1}{2}$ mm. long) that its finding movements can be observed in a conveniently small area, and it is easily reared in large numbers at all times of the year. Moreover, its natural hosts, the eggs of many kinds of Lepidoptera and of a few species of insects of other orders, are very suitable for experiments on finding since, unlike active hosts, they remain where they are placed.

The *Trichogramma* used in the following experiments were from the pure culture reared by Dr Salt on the eggs of the moth *Sitotroga cerealella*. The technique of rearing and obtaining the parasites for experiment has been described by Salt (1934).

For reasons that will appear later, it is essential at the beginning to consider only the movements of a *Trichogramma* on an area where no other females have searched and in the interval of time before the first host is found. In such a uniform area *Trichogramma* does not seek systematically, but moves about at random with respect to the hosts until one of them is perceived. It is not necessary at the moment to say anything further about this random movement since it will be discussed later. As soon as the parasite is able to perceive its host, however, movement ceases to be random and becomes directed towards the host in a manner depending on the sense by which the perception occurs. The means by which a *Trichogramma* perceives its hosts, therefore, has first to be determined.

(*b*) *Perception of the host*

If a female *Trichogramma* is watched when in movement upon graph paper on which are pasted isolated eggs of *Sitotroga cerealella* (which are 0·02 in. long and 0·09 in. across), she can be observed to turn from her line of movement when at a distance of rather less than 0·1 in. from an egg, and to move towards it. Similarly she will turn towards small washed sand grains, objects which, if they have any smell at all, do not have the same smell as the host. This similarity in behaviour towards different types of objects, together with the directness with which the parasite moves towards the egg or sand-grain after turning, suggests that the object has been seen.

That *Trichogramma* does in fact perceive its hosts from a distance by the sense of sight has been proved by experiments in which the intensity of the light was varied while all other factors were kept constant. The details are to be published in a later paper and here it is only necessary to state that over the range of intensities used, the efficiency of finding varied directly with the light intensity.

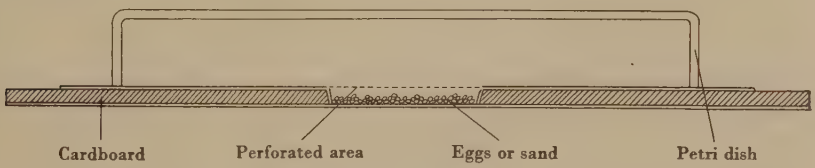


Fig. 2. Vertical section of apparatus used to determine effect of egg-smell on *Trichogramma*. (Approx. natural size.)

There is nothing in these observations, however, to preclude the possibility that smell is an additional means of distance perception, with an effect on movement less noticeable than that of sight. Experiments were performed, therefore, to discover whether *Trichogramma* females are attracted to eggs of *Sitotroga* by their smell.

For this purpose, the central sq. in. in a piece of graph paper $4\frac{1}{2}$ in. square was perforated with a fine needle. The holes made were very minute and numbered between 10 and 20 in each 1/100 sq. in. The central sq. in. of a piece of thick cardboard was cut out, and the window thus formed was closed by pasting a piece of thin paper over one side of the cardboard. When the graph paper and the cardboard were put together, the perforated area lay directly above the cavity in the card (Fig. 2). In the cavity could be placed a thick layer of small washed sand grains or of *Sitotroga* eggs. Ten females of *Trichogramma* were enclosed on the graph paper under the lid of a Petri dish, $3\frac{3}{4}$ in. across; and their movements were watched for 50 min., the number and duration of their visits to the perforated area being especially noted. The experiments took place in daylight at a controlled temperature of 24–25° C. Eight experiments were performed; four using *Sitotroga* eggs and four using sand grains.

The parasites occasionally moved over the perforated area quickly and without turning; that is, they were not mechanically impeded by the perforations. Generally, however, they twisted about and hesitated beside the holes, waving their antennae over and into them. No difference could be detected in the behaviour of the females over the cavities containing eggs and sand respectively. The lack of special attraction to the eggs apparent to observation is confirmed by the numerical results of the experiments which are given in Table 4.

Table 4. *Results of experiments to show influence of egg-smell on* Trichogramma

	Egg area			Sand area		
	Time spent on area			Time spent on area		
Exp.	min.	sec.	No. of visits	min.	sec.	No. of visits
1	9	25	22	5	45	24
2	4	10	24	4	20	23
3	7	10	27	11	5	43
4	5	25	24	8	15	18
Total	26	10	97	29	25	108
Average	6	32	24·25	7	21	27·0

The visits paid to the perforated areas over eggs and over sand did not differ significantly either in number or in duration. It is clear, therefore, that the parasite was not attracted to the vicinity of *Sitotroga* eggs by their smell.

At a later stage in this work it became necessary to use eggs of the moth *Barathra brassicae*, which, unlike eggs of *Sitotroga*, are natural hosts of *Trichogramma*. A series of experiments similar to those just described was therefore done with *Barathra* eggs. Again, no difference was apparent in the behaviour of *Trichogramma* towards the egg and the sand containing cavities respectively. In the course of these experiments, altogether 141 visits were made to the egg area, with an average duration per visit of 10·8 sec.; and 137 visits were made to the sand area, with an average duration of 11·1 sec.

Although the smell of the eggs of *Sitotroga* and *Barathra* appears to have no influence on the movement of the parasite, it is possible that under natural conditions, the adult host leaves an odour about the place of oviposition, and that this odour affects the searching movements of the parasites. To determine whether such traces left behind by moths can help the parasite to find its hosts, experiments were carried out as follows.

Two circles of 1·5 in. diameter, were drawn on a graph-card disk which fitted into a Petri dish. Over one circle was placed a small dish (inner diameter 1·5 in., depth 0·5 in.) in which were placed four or five females of *Sitotroga*. The dish was held down by means of a rubber band, and the Petri dish was placed in the incubator for a period of not less than 40 min. Moths were thus confined over one of the circles on the graph-card disk; in half the experiments they were confined over the left, and in half over the right circle. That over which they

were confined will be called the moth area, the other the clean area (Fig. 3). When the Petri dish was removed from the incubator, the small dish and moths were removed, and four eggs of *Sitotroga* were pasted at a distance of 0·1 in. apart in the centre of each of the two circles.

In a constant temperature room at 25° C., a female *Trichogramma* was then put on the card; the cover of the Petri dish was added; and the parasite was allowed to move about for 25–30 min. Time during which the insect sat on the

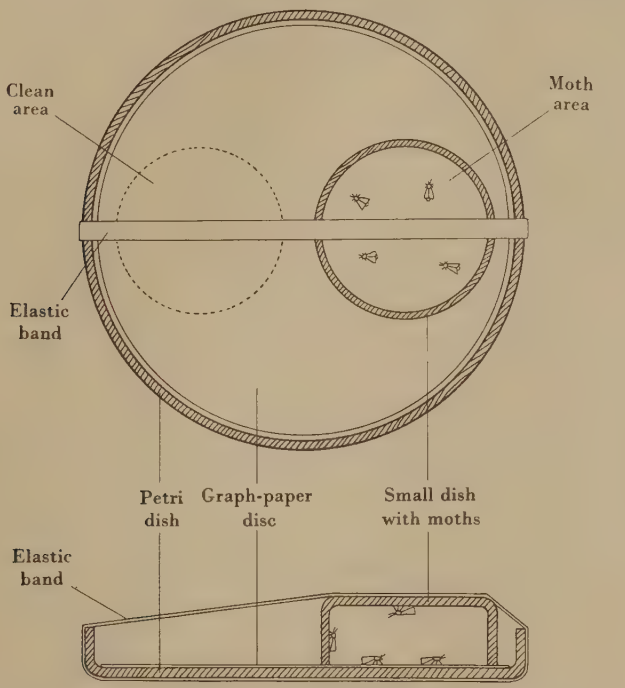


Fig. 3. Plan and vertical section of apparatus used to investigate influence of moth traces on *Trichogramma*.

glass or on an egg was not counted, so that in all cases there were 25–30 min. in which movement was occurring. The experiment was timed with the aid of a stop-watch, the length of time spent by the parasite on the two areas being especially noted. Half-way through the experiment the Petri dish was turned around through 180°, so that the position of the two areas was changed from right to left, or vice versa. Twenty such experiments were performed, with the results shown in Table 5.

Observation of the parasites showed that they waved their antennae more violently and paused more frequently when on the moth area than when on any

Table 5. *The influence of moth-traces on the movement of* Trichogramma

Exp. no.	Total free time min.	Time in Moth area min.	Time in Moth area sec.	Time in Clean area min.	Time in Clean area sec.	% in moth area of total time in both areas	No. of ovipositions in Moth area	No. of ovipositions in Clean area	No of entries into Moth area	No of entries into Clean area
1	25	2	40	1	25	65·3	3	0	4	5
2	28	4	10	4	5	50·5	3	1	7	8
3	25	5	20	1	40	76·2	0	0	22	6
4	25	7	15	1	55	79·1	1	0	22	8
5	25	3	25	0	35	85·4	0	0	12	4
6	24	7	10	2	25	74·8	3	3	24	10
7	25	1	50	0	45	70·9	0	0	9	5
8	25	1	55	0	50	69·7	0	0	8	7
9	25	0	40	1	5	38·1	0	0	5	7
10	25	1	0	1	5	48·0	0	0	5	4
11	30	5	50	2	45	68·0	1	1	24	10
12	28½	10	20	2	35	80·0	4	3	33	11
13	30	3	50	2	15	63·0	0	0	13	11
14	29¾	4	45	0	35	89·1	1	0	19	15
15	30	6	5	0	25	93·5	4	0	19	4
16	30	4	30	2	0	69·2	0	0	13	8
17	30	4	15	1	0	80·9	3	0	14	5
18	30	3	10	0	50	79·1	0	0	8	4
19	30	2	0	1	35	55·8	0	0	12	10
20	30	2	30	0	30	83·3	0	0	10	6
	Total	82	40	30	20	1419·5	23	8	273	138
	Average	4	8	1	31	70·9% in A	1·15	0·4	13·6	6·9

other part of the card. The quantitative results conclusively show the attraction of the moth area. The parasites spent twice as long moving in the moth area as they did in the clean area; they entered the moth area twice as often as the clean area; and they oviposited in the former nearly three times as often as in the latter. The conclusion may be drawn, therefore, that the parasite perceived and was attracted to traces of the moths. Its chance of finding hosts in an area in which the moths had walked was thereby increased.

An experiment similar to those described above was carried out using a *Barathra* female, and it was clear that in this case too, the moth left traces which were attractive to the parasite.

In the above experiments, the chance of finding hosts was influenced by a factor which was not a property, strictly, either of the host environment or of the host egg itself; but which was connected indirectly with the host, since it was a product of the parent moth. It may seem paradoxical that *Trichogramma* is not attracted to host eggs by their own smell but is able to perceive traces left by the insect that laid them. It must be observed, however, that the experiments do not remove the possibility that *Trichogramma* perceives moth traces on the egg-shell, or even the smell of the egg itself when able actually to come into contact with the egg surface. They demonstrate only that the parasites do not perceive eggs by their smell from a distance, and so are not assisted by that sense in their search for hosts.

It has been shown that the perception by *Trichogramma* of traces left by the parent moths may help it to find its host and that its ability to see the hosts may guide it to them from a short distance. It is now necessary to determine whether any part in finding the hosts is played by the sense of touch.

When a seeking *Trichogramma* has seen and has moved towards an egg, it climbs on it and examines it with its antennae; and then, if the egg is acceptable, oviposits. Since the parasite is able to find and to parasitize eggs in darkness, it must be able to perceive them and to recognize them as hosts entirely by the sense of touch. This fact shows that perception by touch is adequate for the recognition of objects as hosts; that it is essential is shown by the experiments of Salt (1935, pp. 427–9). In the experiments referred to, *Sitotroga* eggs were pushed into holes in paper in such a way that each was flush with the surface of the paper and fitted closely to the sides of its hole. The *Trichogramma* females could feel only the slightly convex upper surface of the eggs and were not able to continue their examination around the sides or ends. The eggs, in this case, were not parasitized even though they were perfectly suitable. Contact had been made, but recognition had not followed and the hosts were not "found". Thus, while perception by touch is, obviously, unable to influence the movement of the parasite before a contact, it is necessary for the recognition of an object as a host and so is an essential part of the process of finding.

The first moment of exploration of the egg surface by *Trichogramma* must be regarded as the last stage of the process of finding and, at the same time, the beginning of the process of selection or rejection of the host for oviposition.

To recapitulate—a *Trichogramma* female finds its first host by moving at random in the host-containing area until it comes across chemical traces left by the parent moths or until it sees a host egg, whereupon movement ceases to be at random and a contact between the parasite and the host is likely to follow. The egg is then recognized as a host by the sense of touch.

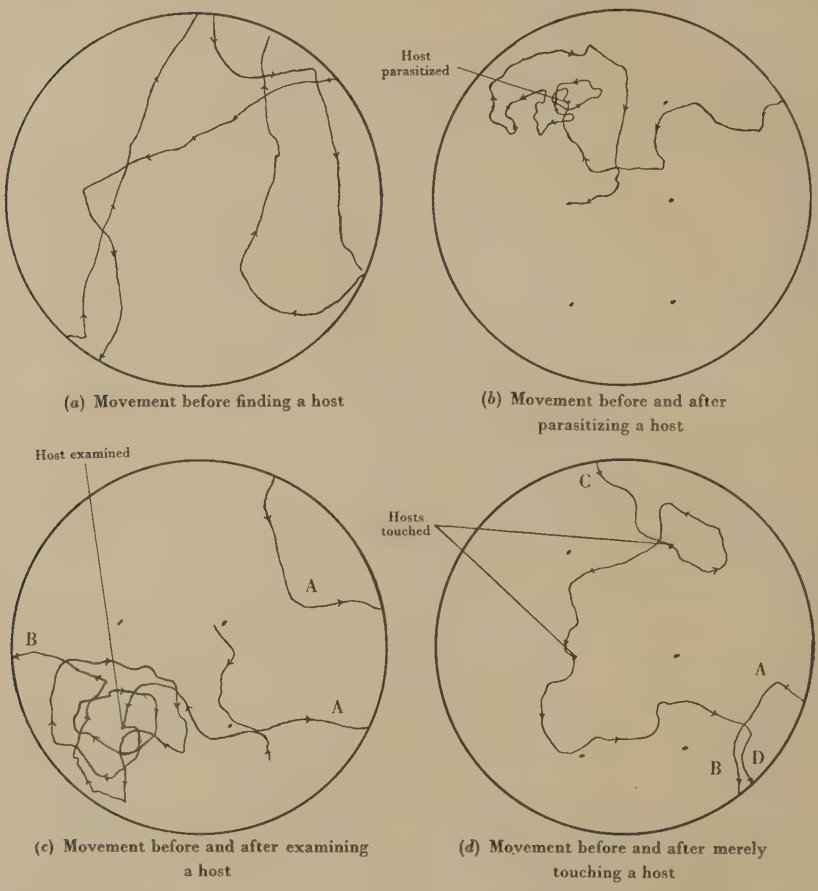
(*c*) *Movement from the first host*

In the preceding section were studied the movements of an isolated female of *Trichogramma* in the act of finding its first host. It would be natural to suppose that the second and succeeding hosts are found by a simple repetition of those movements. That, however, is not the case; and it is now necessary to consider separately how the parasite finds its second and later hosts.

As it moves about at random before finding the first host, the path of the parasite is generally in the form of fairly straight lines or wide curves, the direction of which is only occasionally changed by abrupt turns. A typical path is shown in Fig. 4*a*, a map of the tracks of a female *Trichogramma* which had not yet found a host. The first host is reached by wanderings of this nature; but it is left, after parasitization, by movements which are quite different. The path

of a *Trichogramma* from an egg in which it has just oviposited, takes the form of a much-twisted track, winding round and away from the host (Fig. 4*b*).

Turning movements of this type regularly follow an oviposition. They also occur when the parasite leaves an egg after an examination of more than about



(*a*) Movement before finding a host

(*b*) Movement before and after parasitizing a host

(*c*) Movement before and after examining a host

(*d*) Movement before and after merely touching a host

Fig. 4. Tracks of a female *Trichogramma* (each circle represents a Petri dish $3\frac{3}{4}$ in. across).

2 sec. duration. All the movements made on the graph paper by a *Trichogramma* confined within a Petri dish for a period of 9 min. 10 sec. are shown in Fig. 4*c*; the tracks labelled *A* being those made before a contact with a host, and the spiral track ending at *B* that made after a 20 sec. examination of an egg.

If, however, a host is merely touched for any short period of time less than about 2 sec., the path of the parasite is not so affected and its direction is changed little, if at all, from the path of approach. The absence of effect when the host is merely touched is clearly shown in Fig. 4*d*, where the track *A–B* represents a path in which no hosts were encountered, and that *C–D*, a path on which two hosts were touched but not examined.

Hence, the type of movement by which the second host is found depends upon whether the parasite touches, examines, or parasitizes the first host. If the *Trichogramma* merely touches the egg, the movement is the same after the contact as before; but if it parasitizes or examines the host, the nature of the movement is completely changed.

Hosts may be merely touched, but not examined or attacked, by a parasite in two cases: when the parasite immediately recognizes the host as already parasitized, and when the parasite is not really seeking hosts. If the parasite is actually seeking hosts, and touches one that has not previously been visited, the touch is protracted into an examination and usually leads to oviposition. It follows that when the parasite is not seeking, or finds only parasitized hosts, it moves straight on and so distributes itself broadly; but if it is really seeking hosts and finds one that has not been parasitized, it moves away from it with a turning movement which tends to keep it in that vicinity.

(*d*) *The effect of the turning movement on the chance of finding the next host*

If a *Trichogramma* leaves a host egg on a straight path it treads only a small part of the ground surrounding that egg. If, however, it continually turns as it leaves the host, it covers a great deal more of the area in the vicinity of that host. By turning, therefore, it must increase its chance of encountering any other egg which may be in the immediate vicinity of the first. In order to determine whether there is this postulated effect on the chance of finding a neighbouring host, the following series of experiments was performed.

Thirty *Sitotroga* eggs, chosen at random from a collection of eggs not more than 24 hours old, were pasted on clean graph paper in two rows, 0·9 in. apart, the 15 eggs in each row being 0·2 in. apart (Fig. 5). A female *Trichogramma* was placed on the paper and its movements noted and timed until it had made 26 contacts with the eggs, a contact being either an oviposition, an examination, or a mere touch. Particular note was taken when the insect made a "neighbouring contact", that is, when it moved from one host to a neighbouring host directly, without getting further than 0·2 in. from one egg before touching either of the two neighbouring eggs. For instance, if a *Trichogramma* moved between eggs 3, 4, 5, 6, 8, 9′, as in the diagram, movements 3 to 4 and 5 to 6 would be "neighbouring contacts", but movements 4 to 5, 6 to 8 and 8 to 9′ would not.

Ten experiments of this sort were performed, in daylight, at a temperature between 25 and 27° C. The results are given in Table 6.

Table 6. *The number of neighbouring contacts* (NC) *following oviposition, examination, and touch*

Exp. no.	No. of ovi-positions	No. of NC following ovipositions	No. of examina-tions	No. of NC following examina-tions	No. of touches	No of NC following touches
1	8	3	1	0	16	2
2	7	3	1	1	17	3
3	12	4	2	2	11	2
4	10	4	4	0	11	3
5	13	7	3	1	9	3
6	5	3	1	1	19	9
7	10	7	1	1	14	4
8	15	9	0	0	10	2
9	12	7	1	0	12	1
10	13	9	1	1	11	4
Total	105	56	15	7	130	33

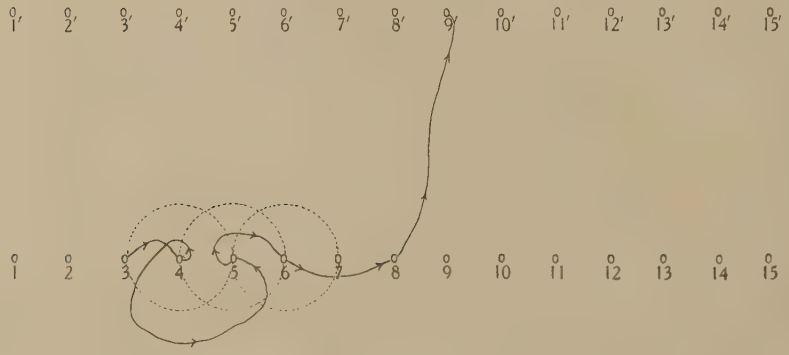


Fig. 5. Arrangement of *Sitotroga* eggs in the final experiment.

From the data it will be seen that the measure of the frequency of neighbouring contacts made by *Trichogramma* when leaving an egg after an oviposition was 56/105 or 53·3%; that made after an examination was 7/15 or 46·6%; and that after a touch was 33/130 or 25·4%. It is clear that the parasites found a neighbouring egg directly on about half the occasions of leaving an egg after an oviposition or an examination, but on only one-quarter of the occasions of leaving an egg after a touch.

In the absence of any other explanation of this difference between the frequencies, the conclusion may be drawn that the turning movement, which has been shown to occur after parasitization and examination of a host but not after a mere touch, is responsible for an increase in the chance of meeting the neighbouring host.

5. Discussion

A parasite finds its host, as any animal must find the thing it seeks, by movements which, until they are influenced by the qualities of the object sought, are random with respect to it. When the qualities are perceived they direct the movement, which thereupon ceases to be random.

The qualities which thus influence the parasite are of two kinds: factors connected with the environment and factors pertaining to the host. It has been shown above (pp. 300–6) that some parasites, when ready to oviposit, do not immediately seek the host itself, but first search for a special kind of situation. Such parasites are attracted by the physical and chemical factors characteristic of different types of environment; for instance, the intensity or kind of illumination, the temperature, humidity, appearance, or smell. In such a case the movement of the parasite ceases to be random long before the host itself is perceived, by reason of the directive influence of the environment.

The way in which the movement towards the environment is influenced depends upon the nature of the factor to which the parasite is reacting. It is generally known, for instance, that if an animal is attracted by an odour, it moves towards the source of the smell on a twisted track; whereas if it is attracted by an appearance, it moves on a straight path to the thing it sees.

Having entered the environment, some parasites appear to search systematically through it, exploring in turn the successive objects in it until they become aware of the host itself. This type of behaviour has been admirably described by the Peckhams (1898, p. 9) in their account of the hunting tactics of *Ammophila urnaria*: "*Urnaria*. . . hunted on bare ground, on the purslane and most of all on the bean-plants. These were examined carefully, the wasp going up and down the stems and looking under every leaf." This type of behaviour, again, exhibits a departure from finding by random movements.

It is clear that the qualities of the individual host that influence the finding movements must vary enormously with the different species of parasite. In the case of *Trichogramma* the effective qualities are the smell of the moth (a factor connected only indirectly with the host) and the shape or mass of the host itself (pp. 307–10). Thus in this insect, two senses, smell and sight, are involved. The hog-louse, *Haematopinus suis* L., is attracted to its host by scent and also, from a short distance, by the heat of the pig (Weber, 1929). Murr (1930) describes how *Habrobracon* finds *Ephestia* larvae chiefly by their smell, which is perceived both as a scent in the air and as a trail on the substratum. The sense by which the trail is perceived, referred to by Murr as "Kontact-Geruchsinn", seems to be the same as that by which *Trichogramma* discerns moth tracks. Further, the sense of touch may be of use in helping a parasite to track its host, in the case of a parasite of a leaf-mining *Phytomyza* larva which has been observed to follow the mine of its host. By whatever sense the

parasite becomes aware of the host, when at last it does so, it no longer moves at random, but orientates itself in some way towards it.

Although many parasites move at random in the host-containing area until they find the first host, the random nature of their movement may be changed when they have found and left it. For instance, as we have seen, the movement of *Trichogramma* is random until the first host is perceived, but after the encounter it is influenced by the contact which has just occurred. Those contacts which result in oviposition or examination are followed by "turning movements" (pp. 312–13) so that, as long as the parasite finds hosts which interest it and which it examines or parasitizes, it continues to turn very frequently as it walks. When, however, it encounters eggs in which it is no longer interested, and which it merely touches, its movements are not affected by the contacts and its course is undisturbed.

Rather similar turning movements have been noticed in preliminary experiments with green-fly parasites (*Ephedrus* sp.). The adult females, after parasitizing a host, moved round about it on a very much twisted track, whereas before the contact with the host they had generally moved straight towards the side of the container nearest the window.

The Peckhams (1898, p. 211) describe and figure the circling movements that are made by several kinds of solitary wasps when they are leaving their newly built nests. *Sphex ichneumonea* flies first in narrow and then in wider circles round the entrance to her nest; species of the genera *Astata* and *Cerceris* likewise twist about their nests for some time before flying off to find their prey. These movements, although superficially similar to the turning movements of *Trichogramma*, serve a different purpose, for they are "locality studies" by which the wasps are enabled to find their nests again when they return.

It emerges from this discussion that a parasite ceases to move at random with respect to its host in at least four circumstances: (1) when it is attracted by the qualities of the host-containing area, (2) when it searches systematically in that area, (3) when it is within the area of perception of the host, and (4) when it moves from the host in a special way. It is to be noticed that all of these influence the movement of the parasite in such a way as to increase its chance of finding a host.

6. Summary

The problem of host-finding is stated and analysed.

It is shown by experiments that the parasites *Alysia manducator* and *Mormoniella vitripennis* are attracted to an environment likely to contain their hosts by qualities of the environment itself, independent of the presence of hosts. Evidence is adduced that several other parasites are likewise first attracted to a special type of situation, in which they then seek their hosts.

Within a host-containing area, the parasite *Trichogramma evanescens* is able to perceive its hosts (eggs of *Sitotroga*) by the sense of sight. It does not

appear to be able to perceive them at a distance by the sense of smell, but it is attracted to traces left by *Sitotroga* females.

Trichogramma normally moves about in straight or widely curving lines with only occasional abrupt turns. On such a path, it finds its first host. When it leaves that host, however, or any host which it has parasitized or examined, it moves quite differently, taking a spiral, twisted path. This change of behaviour greatly increases the frequency of contact between the parasite and its hosts.

ACKNOWLEDGEMENT

I wish here to acknowledge my indebtedness and to express my gratitude to Dr George Salt for the suggestion of this problem, for the use of his culture of *Trichogramma*, and for his constant encouragement and criticism throughout the course of this work.

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THE POPULATION OF PARTRIDGES (*PERDIX PERDIX*) IN GREAT BRITAIN DURING 1936

By A. D. MIDDLETON

Bureau of Animal Population, Oxford University

1. Introduction

This paper records the figures for the partridge population obtained from different estates during 1936 and the 1936-7 shooting season. Previous data of the same kind for most of the estates listed has been published (**1**, **3**) as well as a description of the census techniques used (**2**). The work forms part of a research on game populations carried on by the Bureau of Animal Population with the aid of a grant from Imperial Chemical Industries. I am again indebted to estate owners, shooting men and keepers for their help in keeping records of the partridge population and for giving me facilities for research on game preserves in many parts of the country.

2. Nesting

Table 1 gives the records of nesting and hatching on different estates. Comparison with 1935 figures (**3**) shows an increase in the nesting density in most areas, this being most striking in Norfolk. The density reached on some of the Norfolk estates was the highest for which I have any records: on B 13, 663 nests were actually found on 3000 acres, and on 2700 acres of T 2 there were 511 nests known. Such densities (one nest to between 4 and 5 acres) may probably be regarded as the maximum for partridges under existing conditions in this country.

In most areas the laying and hatching were well up to normal, the average figures being approximately the same as those for 1935 (**3**).

3. Survival of young

Table 2 gives the details of sample counts of young and old birds which were carried out in August in the same manner as in previous years (**2**). Owing to the late harvest in 1936 the counts were mostly done between August 10th and 20th instead of during the first 10 days of August.

Although the nesting density was abnormally high and the hatch successful, the wet summer of 1936 with little sunshine was not favourable for the growth and survival of young partridges. Heavy mortality was experienced during July and August, especially in East Anglia and the Midlands. The losses were exceptionally heavy in north Norfolk, where such high nesting densities were recorded; the central Breckland districts of Norfolk, on the other hand, showed

Table 1. *Records of nesting and hatching of partridges in* 1936

Estate	County	Approx. area in acres	Nests: Estimated total	Nests: No. found	Nests: Known to hatch	Nests: % hatched	Eggs and young: Av. clutch size	Eggs and young: Av. brood size	Eggs and young: % eggs hatched
C 5	Isle of Wight	2,600	150	104	67	64	15·7	14·5	93
R 4	Hampshire	2,400	340	317	235	74	13·6	11·8	88
W 19	Berkshire	6,000	580	405	274	68	14·4	13·4	93
F 1	Wiltshire	5,000	150	78	53	68	—	—	—
S 20	,,	1,450	40	29	14	48	—	—	—
D 12	Oxfordshire	1,400	110	95	53	56	15·9	14·2	89
B 14	,,	3,000	270	181	132	73	14·3	13·6	95
H 7	Shropshire	1,500	145	114	103	90	—	—	—
W 7	,,	2,800	70	32	24	75	16·2	14·8	91
D 4	Lincolnshire		160	150	86	57	14·4	11·4	79
D 2	Northamptonshire	5,000	—	78	41	53	16·2	15·3	94
B 4	Warwickshire	2,700	—	72	67	93	—	—	—
O 1	Nottinghamshire	5,000	650	616	371	60	—	—	—
C 1	Cambridgeshire	900	160	132	122	92	17·2	15·6	91
C 10	Suffolk	1,600	140	128	116	91	15·3	13·0	85
W 1	Norfolk	3,000	510	410	345	84	15·3	14·3	93
W 11	,,	1,400	130	116	104	90	15·4	14·7	95
W 4	,,	5,000	650	586	545	93	16·5	14·7	90
C 8	,,	1,500	150	142	95	67	14·5	12·8	88
W 16	,,	3,000	345	314	281	89	—	—	—
W 16*a*	,,	2,000	235	217	202	93	14·3	13·2	92
B 13	,,	3,000	720	663	594	90	14·8	13·2	89
T 2	,,	2,700	560	511	461	90	15·1	14·0	93
H 5	,,	3,500	480	416	—	—	14·4	12·8	89
R 7	,,	3,000	210	166	137	83	16·6	14·5	87
B 2	Yorkshire	2,000	140	113	63	56	14·1	11·8	—
L 2	Northumberland	2,000	110	28	23	82	15·0	14·3	95
M 1	,,	830	65	32	25	78	15·5	14·8	95
H 8	,,	4,000	300	121	79	65	16·8	15·0	90
G 2	Kirkcudbrightshire	3,000	250	50	44	88	16·1	14·9	92
D 11	Berwickshire	2,800	—	230	187	81	16·2	14·6	90
D 7*a*	Angus	1,500	100	77	73	95	17·6	16·3	92
A 2*a*	Ross-shire	1,500	—	78	69	88	15·5	14·8	96
					Averages	77	15·4	14·0	91

a high survival of young birds, probably due to the porous sandy soil and scanty vegetation on the rabbit grazed heathlands.

On the best arable land of Norfolk the wet summer gave rise to a rank second growth of grasses and clovers on the leys, which, together with the other crops, were continually wet for weeks at a time—very unfavourable conditions for young partridges. The south of England did not suffer to the same extent from continuous wet weather and the counts show more uniform results and lower mortality in Hampshire. Some estates in the north of England and in Scotland also show a fairly high ratio of young to old.

In East Anglia mortality among the young continued during and after the time at which the count was made, making the final crop of young birds lower than is indicated by the August counts. Many birds examined during this period had died from a form of pneumonia or from gapes (*Syngamus trachea*).

Table 2. *Sample counts of old and young partridges made in August* 1936

Estate	County	Counted in August: Old	Young	Coveys	Young : old ratio	% coveys surviving	Av. young per surviving covey
C 5	Isle of Wight	119	364	46	3·06	77	7·9
R 4	Hampshire	237	638	78	2·70	66	8·2
L 1	,,	104	257	32	2·47	62	8·0
L 4	,,	91	249	30	2·74	66	8·3
L 15	,,	289	871	86	3·01	61	10·1
R 2	,,	166	519	55	3·12	66	9·4
M 2	,,	126	332	38	2·68	60	8·7
W 19	Berkshire	653	1534	183	2·34	56	8·4
F 1	Wiltshire	98	311	38	3·17	78	8·2
S 20	,,	47	49	9	—	—	—
B 25	,,	44	90	11	2·05	50	8·2
D 12	Oxfordshire	107	303	26	2·83	49	11·7
B 14	,,	131	379	47	2·90	72	8·1
W 18	Gloucestershire	100	427	44	4·27	88	9·7
H 7	Shropshire	215	200	27	0·93	25	7·4
W 7	,,	102	120	16	1·18	32	7·5
N 5	Leicestershire	61	147	19	2·41	62	7·7
D 4	Lincolnshire	180	211	45	1·17	50	4·7
O 1	Nottinghamshire	314	393	54	1·25	34	7·3
H 9	Essex	32	82	12	2·56	75	6·8
C 1	Cambridgeshire	191	479	62	2·50	65	7·7
S 1	,,	520	602	111	1·16	43	5·4
C 10	Suffolk	216	572	67	2·65	63	8·6
W 1	Norfolk	248	546	82	2·20	66	6·7
W 11	,,	106	448	46	4·22	87	9·7
W 4	,,	175	545	60	3·11	69	9·0
K 2	,,	37	147	13	3·96	70	11·3
W 16	,,	259	365	48	1·41	37	7·6
W 16*a*	,,	185	317	47	1·72	51	6·7
B 13	,,	81	180	26	2·22	64	6·9
T 2	,,	328	577	72	1·76	44	8·0
H 5	,,	131	190	25	1·43	38	7·6
R 7	,,	250	591	72	2·37	58	8·2
B 2	Yorkshire	217	451	58	2·08	54	7·8
L 2	Northumberland	156	368	44	2·36	56	8·4
M 1	,,	65	222	25	3·41	77	8·9
H 8	,,	147	390	41	2·65	56	9·5
G 2	Kirkcudbrightshire	86	334	30	3·88	70	11·1
D 7	Angus	124	267	37	2·15	60	7·2
A 2*a*	Ross-shire	159	742	76	4·66	95	9·8
				Averages	2·53	61	8·3

4. Shooting season, 1936–7

Comparable shooting records for the past three seasons are shown in Table 3. The numbers killed were generally lower than in 1935–6, except on some of the southern, northern and Breckland estates, but the drop is not so great as might have been expected from the mortality among the young. The nesting stocks at the beginning of 1936 were so extremely high (Table 1) that even with low or moderate production of young there was still a good surplus for shooting in the autumn. If the survival of young had been as good as in 1935 (**3**) there would, in Norfolk for example, have been an enormous population.

Towards the end of the 1936–7 season and during the spring of 1937 there was heavy mortality from disease among the adult partridges in East Anglia, particularly in North Norfolk, and the nesting stock for 1937 has been greatly reduced. An account of this will be published later.

5. SUMMARY

Records of nesting, summer sample counts and kills for partridges on many estates are tabulated, to continue previous records of the same kind. The nesting density in many areas seems to have reached a maximum in 1936, but an unfavourable summer was associated with high mortality among the young and numbers killed in the shooting season were generally smaller than in 1935.

Table 3. *Numbers of partridges killed on different estates from* 1934 *to* 1936

Estate	County	Approx. area in acres	Shooting seasons 1934–5	1935–6	1936–7
C 5	Isle of Wight	2,600	624	568	419
L 4	Hampshire	1,150	524	394	375
M 2	,,	2,700	514	613	389
R 2	,,	4,000	1,086	355	2,023
L 15	,,	3,000	831	461	820
F 1	Wiltshire	5,000	354	373	159
G 5	Hertfordshire	1,200	97	88	35
K 1	,,	1,800	207	240	265
C 1	Cambridgeshire	3,500	1,207	2,134	1,164
S 1	,,	10,000	2,398	4,007	2,601
H 9	Essex	3,000	720	945	362
C 10	Suffolk	1,600	758	506	454
O 2	,,	11,000	2,422	2,181	2,429
W 1	Norfolk	3,000	1,341	2,001	1,220
W 11	,,	10,000	2,074	2,847	2,670
W 4	,,	6,700	945	1,376	2,281
H 3	,,	17,000	4,404	5,151	2,549
W 16	,,	5,000	1,146	1,676	1,261
W 14	,,	4,800	1,596	1,655	1,872
B 13	,,	3,000	2,202	2,602	1,648
T 2	,,	2,700	2,113	2,477	1,472
H 5	,,	4,000	2,545	3,921	2,001
R 7	,,	3,000	263	248	304
B 14	Oxfordshire	4,700	1,058	746	655
D 2	Northamptonshire	5,000	640	556	405
H 1	Worcestershire	1,700	111	111	27
H 7	Shropshire	2,000	550	473	141
W 7	,,	11,000	1,860	1,519	373
N 5	Leicestershire	1,200	122	176	118
O 1	Nottinghamshire	5,000	2,964	2,061	941
N 1	Yorkshire	2,000	269	290	153
L 2	Northumberland	2,000	392	297	280
M 1	,,	830	206	283	119
H 8	,,	4,000	655	256	452
G 2	Kirkcudbrightshire	3,000	296	224	235
D 11	Berwickshire	8,000	1,909	841	1,904
M 12	Fife	2,370	664	366	759
B 23	,,	2,000	615	375	316
W 10	Banff	4,000	592	210	563
	Totals	168,550	43,274	45,603	36,214

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THE FOOD OF ADULT PARTRIDGES, *PERDIX PERDIX* AND *ALECTORIS RUFA*, IN GREAT BRITAIN

By A. D. MIDDLETON and HELEN CHITTY

Bureau of Animal Population, Oxford University

(*With Plates* 9 *and* 10 *and* 1 *Figure in the Text*)

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1. Introduction

The work on which this paper is based forms part of a research into the ecology of game birds carried on by the Bureau of Animal Population. This research has been made possible by a grant from Imperial Chemical Industries and by the donations of landowners and others interested in game preservation. Our thanks are due not only to those who have helped financially but to shooting men and keepers in all parts of the country who give facilities for this work on their estates and send us birds for examination.

The sorting out and identification of most of the seeds and other plant food was done by E. Arthurs of the Oxford Botanical Department, while the identification and volumetric measurements of insects were carried out by John Ford and E. W. Aubrooke in the Hope Department of Entomology at Oxford. We are greatly indebted to them for this assistance.

The present paper deals only with the food of adult wild partridges. Material collected from young partridges is being analysed and the results will be published later. Young birds are classed as "adults" when killed any time after the opening of the shooting season, September 1st, but a record has been kept of whether the birds examined were young adults or old birds (over 16 months old) except when crops were sent in separately by keepers and others without data. Altogether, 429 adult grey partridges (*Perdix perdix*) and 29 red-legged partridges (*Alectoris rufa*) have been examined for food. The crop contents only have been used for this purpose as food found in the gizzard is usually in such a finely divided state as to be almost unrecognizable and certainly of no value for quantitative work. There is no reason to doubt that the crop contents alone form a truly representative sample of the food eaten. As there is no evidence to suggest that some food items pass more quickly than others from the crop

to the gizzard, it may safely be assumed that the material found in the crop of a partridge at death (most of the birds were shot or killed accidentally) is the food taken a short time before.

Most of the crops were taken from shot partridges and, as the shooting season is from September 1st to January 31st, the numbers examined from September to January are much greater than for other months; outside the shooting season we have had to rely on birds killed accidentally, for instance by telephone wires and grass cutters or by disease (although most diseased birds have nothing in their crops at death). Crops have been collected during the years 1933–7 and for the purposes of showing seasonal differences throughout the year the data have been combined, as in Fig. 1.

The contents of each crop were stored in tubes of 10% formalin to be sorted and examined later. The routine for sorting and identification of the various items was as follows. The whole crop contents from formalin were washed, spread out on blotting-paper and placed on a warm stage until the excess water had evaporated, leaving any green leaves at approximately the same dryness as when fresh. The green leaves, flowers and roots were then sorted out from seeds, etc., and measured volumetrically in a small measuring cylinder by displacement of water; by this means it was possible to measure the volume of any quantity greater than 0·05 c.c., but any volumes less than 0·05 c.c. were given the conventional figure of 0·025 c.c. At this stage any insects in the crop were removed and put into 70% alcohol to be dealt with later. The rest of the material (seeds) was dried further until it was possible to sort out the individual seeds. The seeds of each species were then sorted and counted, some being identified at once and others kept in a dry state for further examination.

All the data for each partridge and its crop contents are recorded on cards and the original material preserved in the Bureau of Animal Population.

The figures for volume and weight of seeds were obtained after most of the crops had been sorted, by measuring and weighing a convenient quantity (0·5–5 c.c. according to the size of seed) and counting the number of seeds in the measured sample. By this means we were able to calculate the volume or weight of very small quantities of seeds which would have been very difficult to measure directly for each crop.

2. The partridge habitat

Since the partridges from which the crops were taken came from so many scattered localities in widely differing types of country, it is not possible to give an accurate analysis of the environment, for correlation with the food items chosen by the birds. It may be useful, however, to give a general picture of the kind of habitats in which the highest densities of partridges are found, together with a brief summary from field observation of the feeding habits of partridges at different seasons of the year.

The most favourable habitat for partridges is arable land on dry soils such

as sand and gravel, chalk or brick earth, associated with low rainfall. As the majority of the partridges dealt with in this paper came from preserved estates where conditions were suitable, it follows that most of them had lived on cultivated land with a great diversity of crops. There would be corn crops (wheat, barley and oats), root crops (turnips, mangolds, swedes, sugar beet, potatoes, etc.), green forage and hay (grasses, clover, lucerne, sainfoin, vetches, etc.), permanent pastures and small patches of waste land, hedge banks, etc., with a variety of uncultivated grasses and weeds. Normally farm crops are grown in small enough units (10–20 acres) to give the adult partridges a choice of several different crops, such as corn, grass and roots, within their cruising range; although the movement of young birds up to 4 or 6 weeks may be confined entirely to a single crop or field of corn or grass.

The most important differences in the environment which would be expected to affect the available food supply are not so much the differences in crops in the various areas dealt with, but the seasonal changes due to the growth and cultivation of the crops. In analysing the results of our findings in the crops of the partridges we have divided the year into five periods based on the changes which normally take place in the environment. The following summary of the conditions affecting the food supply during those five periods applies to most areas where about half or more of the land is cultivated, but it is obvious that on large areas of permanent grassland or downland the seasonal changes do not vary the food supply to the same extent.

(1) *September.* This month is taken separately as the first period of the partridge's year because the young birds can be regarded as adult at this time, the shooting season opens and there is a sudden change in the environment due to the harvesting of all corn crops. Throughout September in any year there is an abundant variety of food. The stubbles from which corn has been harvested are covered with scattered grain and rapidly growing annual weeds such as knotgrass, orache and chickweeds, while ungrazed grass areas provide ample seed supplies.

(2) *October November.* The autumn ploughing of stubbles which have not been laid down to grass or clover, removes a large proportion of the feeding range during this period. The clover and grass leys which have been cut during the summer are also ploughed by this time for autumn sown corn crops. This means that on any well-cultivated arable area, where the four-course system is practised, approximately one-half of the total area is ploughed, and there is very little food for partridges on freshly ploughed land. The feeding grounds left are the unploughed stubbles, mostly sown down with clover or grass for next year's crop, some root fields, permanent pasture and long term leys such as lucerne.

Root fields usually carry a fairly heavy crop of weeds at this time of the year so there is a good deal of food for partridges in them. In areas where sugar beet is grown, especially in Norfolk, the harvesting of sugar-beet provides a

new source of food, as the crowns of the beet are cut off and left lying about the fields until they are ploughed in later in the year. Partridges rarely eat the growing roots, but readily peck out the cut surfaces of the sugar-beet crowns.

(3) *December February.* The most significant change in the food supply during this period is the almost complete disappearance of corn and reduction in the available seeds. The corn on the stubbles disappears quickly, partly by being eaten and partly by germination; and, as the partridge does not scratch into the soil for food, very little freshly sown corn is eaten. All of the temporary stubbles will be ploughed, as well as many of the old root fields. Thus apart from the sown down stubbles, permanent grass and a few old root fields, most of the land is ploughed.

The fact that partridges are always to be found feeding on the old stubbles or "leys" at this time of the year has led to the belief that these are the ideal feeding grounds. Actually, on a well-cultivated area there is very little food to be found anywhere else, so the partridges probably have no choice in the matter. As the grass and clover grows on the old stubbles, the seed-bearing weeds are swamped under the vegetation, especially in a mild winter, so by the end of January there is very little except greenstuff available on them.

(4) *March–May.* During March and April the food supply of the partridge is probably more restricted than at any other time of the year. There is practically nothing but green food available. On arable land a large area is still bare ploughed ground although by the beginning of May the corn, grass and clover crops will be growing rapidly. It is not, however, until the end of May that any quantity of seeds of weeds or grasses can be expected. During this period it is very difficult to obtain data about the food of partridges; they are all paired and starting to nest, there is no shooting and very few birds are killed accidentally by farming operations, etc.

(5) *June August.* The rapid growth and seeding of weeds, grasses and corn provides a wide choice and an abundance of food during this period. The only unproductive areas are the root field and fallows, which are constantly cultivated, giving little food or cover for partridges. But standing corn and long grass will provide ample accommodation for very large numbers of partridges on any normal area.

3. Results of crop examinations

Table 1 and Fig. 1 show the seasonal change in the food of adult partridges throughout the year and the percentage by volume of the main types of food eaten. Perhaps most striking are the large quantities of green food eaten during the winter and spring months and the very low percentage of animal food. For some reason, partly due to the publications of Collinge (**1**, **4**), insects have for a long time been regarded as an important and even essential part of the food of partridges. Collinge states that his examinations (not published in detail) showed 40·5% of the food to be animal matter. The figures shown in Table 1

do not support this conclusion. It will be seen that the only period when animal food forms an appreciable proportion (11·8%) of the total, is in the summer months; but during most of this period the young partridges, accompanied by their parents, take a very much higher percentage of animal food (unpublished notes).

It seems, therefore, that even when insect food is abundant, the adult birds do not show any preference for it. Of 398 partridges examined between September and May, only 29 contained any animal food and this represented only 0·2% of the total volume of food eaten. Yeatter(**7**) obtained similar evidence in America that only a small proportion of the food is animal matter.

Table 1. *Percentage by volume of different kinds of food eaten by adult partridges throughout the year*

	Sept.		Oct.–Nov.		Dec.–Feb.		Mar.–May		June–Aug.		Mean % for year
No. of crops examined	177		175		34		12		31		
Total volume	506·88 c.c.		631·91 c.c.		187·71 c.c.		98·92 c.c.		140·00 c.c.		
	c.c.	%	c.c.	%	c.c.	%	c.c.	%	c.c.	%	
Grass, clover and leaves	50·25	9·9	167·25	26·5	127·92	68·0	91·15	92·2	20·10	14·3	42·2
Flowers and buds	4·49	0·9	1·00	0·2	—	—	5·93	6·0	40·24	28·7	7·2
Roots (sugar-beet, etc.)	1·80	0·4	103·55	16·4	24·98	13·3	0·50	0·5	—	—	6·1
Seeds (grasses and weeds)	60·35	11·9	218·43	34·5	33·49	17·8	1·17	1·2	53·94	38·5	20·8
Grain (wheat, barley, oats and buckwheat)	387·04	76·3	141·44	22·4	1·32	0·7	0·15	0·1	9·18	6·5	21·2
Animal food (mainly insects)	2·94	0·6	0·24	0·04	—	—	0·02	0·02	16·54	11·8	2·5

The food taken in September differs greatly from that at other times of the year in the quantity of grain; this is obviously due to the large areas of stubble from which the corn has been harvested. Such stubbles, whether or not they carry clover or grass crops for next year, are usually rather bare of seeding weeds during early September, but have an abundance of scattered grain. There is little doubt that the partridges make the best use of this easily obtained food supply while it lasts.

The figure for October–November clearly shows the decline in available grain food, partly balanced by an increase in the quantity of weed and grass seeds. This follows logically, as many stubbles are ploughed in and those remaining develop a rich crop of seeding weeds such as knotgrass (*Polygonum aviculare*), bindweed (*P. Convolvulus*) and orache (*Atriplex patula*). The considerable proportion of roots (16·14%) during this period is mainly due to sugar-beet, the partridges pecking out the pulp from the cut-off crowns when the beet is harvested. The fresh growth of the clovers and grasses on the old stubbles would account for the increase in green food.

From December to February there is an obvious restriction of the grain and seed supply. Roots (still mainly sugar-beet) continued to provide an alternative, but the majority of the food has to be greenstuff.

During the March May period there is very little seed food of any kind available, grass, leaves, flowers and buds making up over 98% of the partridge's food.

The summer months (June-August) bring a quick change in the figures, flowers and buds being abundant, many of the grasses and weeds seeding

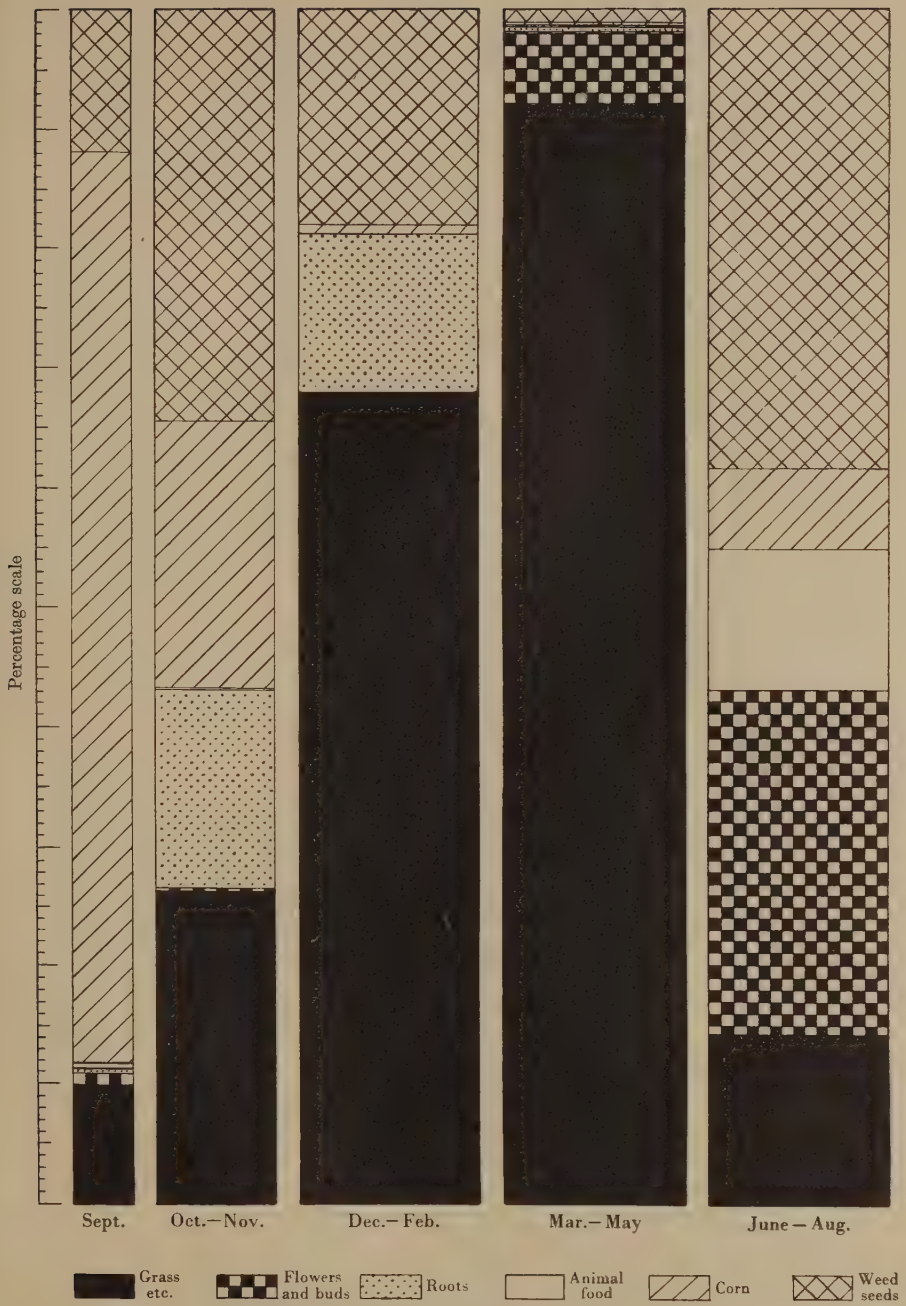


Fig. 1. The percentage composition by volume of the food of adult wild partridges at different seasons of the year.

profusely, and standing corn providing plenty of unripe grain from the shorter or fallen stalks. Insects, too, are found in many crops.

(*a*) *Seeds and grain*

Table 2 shows the relative importance of different species of seeds and grain during the different seasons. As the volumes have been worked out as percentages of the *total* volumes of food, the seeds of individual species show a very low percentage from December to May when the bulk of the food is greenstuff (Fig. 1). Apart from the four cultivated seeds (wheat, barley, oats and buckwheat) those of *Polygonum* seem to be the favourite. *P. aviculare* and *P. Convolvulus* are two of the most common weeds on autumn stubbles throughout Britain, so it is difficult to know whether their use by the partridges is a matter of availability or preference. Small quantities of grass seeds occur in many crops throughout the year, the most abundant being the common grasses, *Poa annua*, *Lolium italicum*, *Festuca pratensis* and *Bromus arvensis*. Orache (*Atriplex patula*) and goosefoot (*Chenopodium album*) are frequently found in late autumn crops, being weeds common to both stubbles and root fields. The two chickweeds, *Stellaria media* and *Cerastium vulgatum*, are eaten throughout the summer and autumn, the ripe and unripe capsules being taken whole by the birds as the seeds are very small. The capsules of wild pansy (*Viola tricolor*) and scarlet pimpernel (*Anagallis arvensis*) are also taken frequently although not in great quantities. It is curious that so little charlock seed (*Brassica arvensis*) is eaten, as this is one of the commonest weeds in many areas and other birds, such as wood-pigeons, eat it readily.

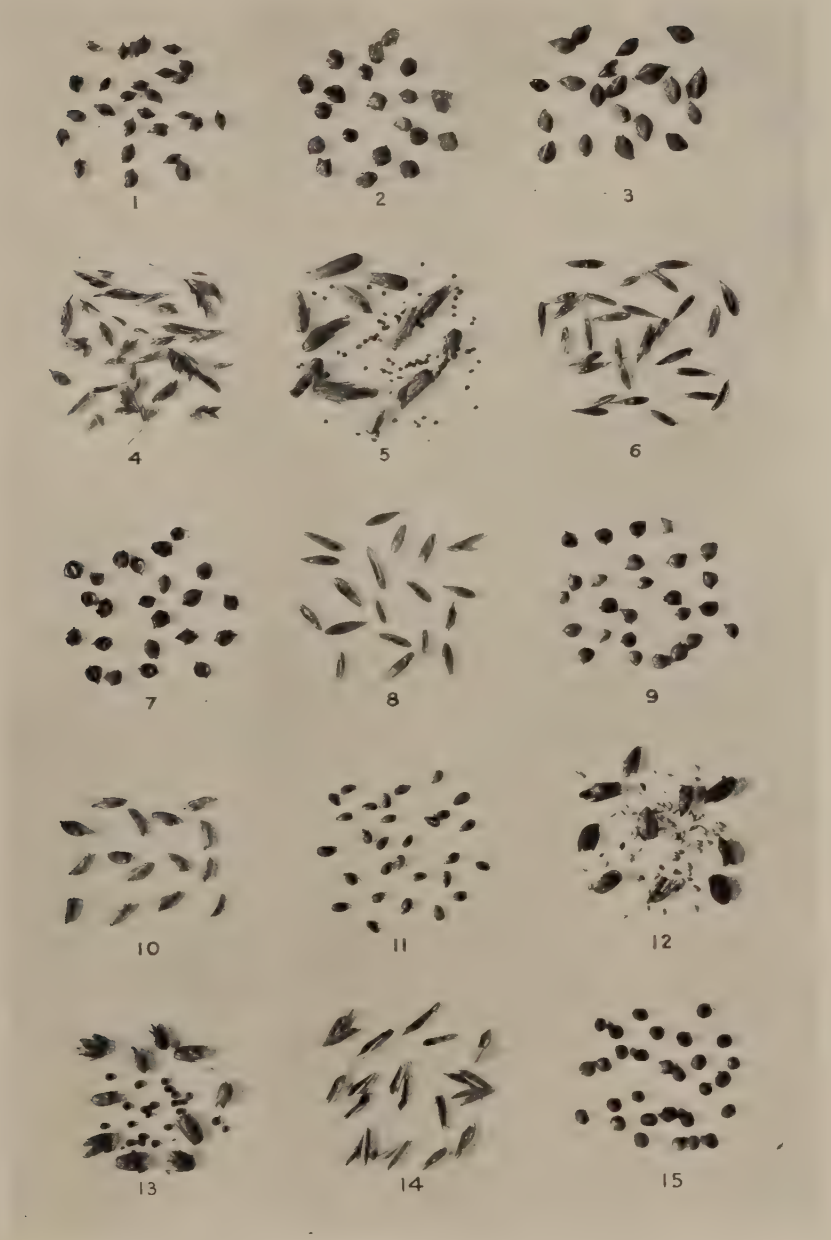
(*b*) *Flowers and buds*

It will be seen from Fig. 1 and the following table that flowers and flower buds are an important item in the food of the partridge during the summer months. The flowers were not enumerated specifically in the individual crop analyses, the volume alone being measured in each crop, but the following species were commonly found: buttercup, *Ranunculus* sp.; hawkbit, *Leontodon autumnalis*; cat's ear, *Hypochaeris radicata*; sowthistle, *Sonchus oleraceus*; chickweed, *Stellaria media*; charlock, *Brassica arvensis*; poppy, *Papaver* sp.; hawk's beard, *Crepis virens*.

	Sept.	Oct.–Nov.	Dec.–Feb.	Mar.–May	June–Aug.
No. of occurrences	14	7	—	2	16
Percentage occurrence	7·9	4·0	—	16·7	51·6
Percentage of total volume	0·9	0·2	—	6·0	28·8

Seeds illustrated in Plate 9.

(1) Knotgrass (Knotweed), *Polygonum aviculare*; (2) Orache, *Atriplex patula*; (3) Black Bindweed, *Polygonum Convolvulus*; (4) Common Meadow Grass, *Poa annua*; (5) Mouse-ear Chickweed, *Cerastium vulgatum* (capsules); (6) Italian Ryegrass, *Lolium italicum*; (7) Pale persicaria, *Polygonum lapathifolium*; (8) Meadow Fescue, *Festuca pratensis*; (9) Buttercup, *Ranunculus* sp.; (10) Great Knapweed, *Centaurea Scabiosa*; (11) Red Galeopsis, *Galeopsis Ladanum*; (12) Common Eyebright, *Euphrasia officinalis* (capsules); (13) Chickweed, *Stellaria media* (capsules); (14) Field Bromegrass, *Bromus arvensis*; (15) Common Fumitory, *Fumaria officinalis*.



Phot. 1. Seeds found most commonly in partridge crops. Natural size.
(*See list on opposite page*)

Table 2. *Volume and number of occurrences of principal seeds and grain found in adult partridge crops at different seasons*

	No. of occurrences	Av. no. of seeds per crop	Total vol. in c.c.	% volume	% occurrence
Sept.: 177 crops, total volume 506·88 c.c.					
Barley, *Hordeum sativum*	79	78	238·00	47·0	44·6
Wheat, *Triticum*	70	41	106·41	21·0	39·6
Oats, *Avena sativa*	32	26	24·59	4·9	18·1
Buckwheat, *Polygonum fagopyrum*	9	10	18·04	3·6	5·1
Rye-grass, *Lolium italicum*	18	41	10·74	2·0	10·2
Knotgrass, *Polygonum aviculare*	73	49	8·50	1·7	41·2
Bindweed, *Polygonum Convolvulus*	74	12	6·34	1·2	41·8
Fescue grass, *Festuca pratensis*	6	272	3·67	0·7	3·4
Meadow grass, *Poa annua*	13	284	3·51	0·7	7·3
Hempnettle, *Galeopsis Ladanum*	8	165	3·18	0·6	4·5
Eyebright, *Euphrasia officinalis*	7	118	3·01	0·6	4·0
Fumitory, *Fumaria officinalis*	7	74	2·22	0·4	4·0
Bladder campion, *Silene inflata*	29	40	2·07	0·4	16·4
White campion, *Lychnis alba*	—	—	—	—	—
Other seeds (*see separate list*)	—	—	17·11	3·4	—
Oct.–Nov.: 175 crops, total volume 631·91 c.c.					
Knotgrass, *Polygonum aviculare*	96	570	129·02	20·4	54·9
Barley, *Hordeum sativum*	32	69	85·19	13·5	18·3
Wheat, *Triticum*	22	58	47·04	7·4	12·6
Orache, *Atriplex patula*	59	209	37·88	6·0	33·7
Bindweed, *Polygonum Convolvulus*	62	55	24·52	3·9	35·4
Oats, *Avena sativa*	15	21	9·21	1·5	8·6
Pale persicaria, *Polygonum lapathifolium*	3	1019	9·15	1·4	1·7
Meadow grass, *Poa annua*	31	192	5·66	0·9	17·7
Mouse-ear chickweed, *Cerastium vulgatum*	17	13	2·09	0·3	9·7
Goosefoot, *Chenopodium album*	11	136	1·14	0·2	6·3
Charlock, *Brassica arvensis*	9	35	1·07	0·2	5·1
Other seeds (*see separate list*)	—	—	7·90	1·2	—
Dec.–Feb.: 34 crops, total volume 187·71 c.c.					
Knotgrass, *Polygonum aviculare*	6	2021	28·67	15·6	17·6
Orache, *Atriplex patula*	3	342	3·16	1·7	8·8
Wheat, *Triticum*	2	15	1·11	0·6	5·9
Meadow grass, *Poa annua*	9	104	0·89	0·5	26·4
Yellow rattle, *Rhinanthus crista-galli*	1	83	0·54	0·3	2·9
Bindweed, *Polygonum Convolvulus*	5	4	0·14	0·1	14·7
Barley, *Hordeum sativum*	1	3	0·12	0·1	2·9
Other seeds (*see separate list*)	—	—	0·18	0·1	—
Mar.–May: 12 crops, total volume 98·92 c.c.					
Knotgrass, *Polygonum aviculare*	1	181	0·42	0·4	8·3
Chickweed, *Stellaria media*	2	37	0·25	0·3	16·7
Meadow grass, *Poa annua*	4	50	0·19	0·2	33·3
Perennial rye-grass, *Lolium perenne*	1	70	0·19	0·2	8·3
Barley, *Hordeum sativum*	1	4	0·15	0·2	8·3
Other seeds (*see separate list*)	—	—	0·12	0·1	—
June–Aug.: 31 crops, total volume 140·00 c.c.					
Meadow grass, *Poa annua*	17	1270	20·51	14·7	54·8
Mouse-ear chickweed, *Cerastium vulgatum*	15	117	16·30	11·6	48·3
Wheat, *Triticum*	4	53	7·82	5·6	12·9
Buttercup, *Ranunculus* sp.	8	250	4·65	3·3	25·8
Great knapweed, *Centaurea Scabiosa*	2	324	3·35	2·4	6·4
Brome grass, *Bromus arvensis*	4	360	2·60	1·9	12·9
Fescue grass, *Festuca pratensis*	2	441	1·98	1·4	6·4
Oats, *Avena sativa*	2	20	1·21	—	6·4
Red fescue grass, *Festuca rubra*	1	800	0·91	0·7	3·2
Chickweed, *Stellaria media*	11	22	0·81	0·6	35·4
Sandwort, *Arenaria serpyllifolia*	5	34	0·66	0·5	16·1
Other seeds (*see separate list*)	—	—	2·32	1·7	—

SEEDS OCCURRING IN VERY SMALL QUANTITIES

Sept.

Buttercup, *Ranunculus* sp.; poppy, *Papaver* sp.; charlock, *Brassica arvensis*; black mustard, *B. nigra*; cut-leaved mignonette, *Reseda lutea*; field pansy, *Viola tricolor*; thyme-leaved sandwort, *Arenaria serpyllifolia*; mouse-ear chickweed, *Cerastium vulgatum*; chickweed, *Stellaria media*; corn spurry, *Spergula arvensis*; black medick, *Medicago lupulina*; sainfoin, *Onobrychis sativa*; field pea, *Pisum* sp.; tormentil, *Potentilla erecta*; salad burnet, *Poterium Sanguisorba*; great knapweed, *Centaurea Scabiosa*; hawkbit, *Leontodon autumnalis*; prickly sowthistle, *Sonchus asper*; hawk's beard, *Crepis virens*; common pimpernel, *Anagallis arvensis*; viper's bugloss, *Echium vulgare*; scorpion grass, *Myosotis arvensis*; toadflax, *Linaria vulgaris*; pointed toadflax, *L. Elatine*; common hemp-nettle, *Galeopsis Tetrahit*; ribwort plantain, *Plantago lanceolata*; annual knawel, *Scleranthus annuus*; white goosefoot, *Chenopodium album*; common orache, *Atriplex patula*; pale persicaria, *Polygonum lapathifolium*; dwarf spurge, *Euphorbia exigua*; sweet vernal grass, *Anthoxanthum odoratum*; slender foxtail, *Alopecurus agrestis*; fine bent-grass, *Agrostis tenuis*; false-oat grass, *Arrhenatherum avenaceum*; couch-grass, *Agropyrum repens*; field brome, *Bromus arvensis*.

Oct.–Nov.

Rockcress, *Arabis hirsuta*; shepherd's purse, *Capsella Bursa-pastoris*; field pansy, *Viola tricolor*; bladder campion, *Silene inflata*; white campion, *Lychnis alba*; thyme-leaved sandwort, *Arenaria serpyllifolia*; chickweed, *Stellaria media*; corn spurry, *Spergula arvensis*; black medick, *Medicago lupulina*; lucerne, *Medicago sativa*; field pea, *Pisum* sp.; tormentil, *Potentilla erecta*; fool's parsley, *Aethusa Cynapium*; hedge parsley, *Torilis nodosa*; hawkbit, *Leontodon autumnalis*; lesser bindweed, *Convolvulus arvensis*; common pimpernel, *Anagallis arvensis*; scorpion grass, *Myosotis arvensis*; basil-thyme, *Calamintha Acinos*; common hemp-nettle, *Galeopsis Tetrahit*; greater plantain, *Plantago major*; ribwort plantain, *P. lanceolata*; annual knawel, *Scleranthus annuus*; dwarf spurge, *Euphorbia exigua*; slender foxtail, *Alopecurus agrestis*; meadow foxtail, *Alopecurus pratensis*; Yorkshire fog, *Holcus lanatus*; Italian ryegrass, *Lolium italicum*; field brome, *Bromus arvensis*; meadow fescue, *Festuca pratensis*.

Dec.–Feb.

Wild radish, *Raphanus Raphanistrum*; bladder campion, *Silene inflata*; white campion, *Lychnis alba*; mouse-ear chickweed, *Cerastium vulgatum*; chickweed, *Stellaria media*; corn spurry, *Spergula arvensis*; ribwort plantain, *Plantago lanceolata*; annual knawel, *Scleranthus annuus*; oats, *Avena sativa*.

Mar.–May

Bladder campion, *Silene inflata*; white campion, *Lychnis alba*; dove's-foot geranium, *Geranium molle*; orache, *Atriplex patula*; black bindweed, *Polygonum Convolvulus*.

June–Aug.

Common fumitory, *Fumaria officinalis*; shepherd's purse, *Capsella Bursa-pastoris*; field pansy, *Viola tricolor*; pearlwort, *Sagina* sp.; dove's-foot geranium, *Geranium molle*; black medick, *Medicago lupulina*; saxifrage, *Saxifraga* sp.; dandelion, *Taraxacum officinale*; lesser hawkbit, *Thrincia hirta*; common pimpernel, *Anagallis arvensis*; basil-thyme, *Calamintha Acinos*; orache, *Atriplex patula*; sorrel dock, *Rumex Acetosa*; knotgrass, *Polygonum aviculare*; dwarf spurge, *Euphorbia exigua*; sweet vernal grass, *Anthoxanthum odoratum*; meadow foxtail, *Alopecurus pratensis*; Yorkshire fog, *Holcus lanatus*; barley, *Hordeum sativum*; couch grass, *Agropyrum repens*; ryegrass, *Lolium perenne* and *italicum*.

(*c*) *Roots*

Practically all the root food found in crops was certainly sugar beet (*Beta* sp.) although it is possible that there were fragments of mangold or swede mixed with some samples. Most of the crops containing sugar-beet came from Norfolk,

where sugar-beet is grown on a large scale. It will be seen from Fig. 1 and the following summary that sugar-beet is an important item during the winter months when seed and grain is scarce.

	Sept.	Oct.–Nov.	Dec.–Feb.	Mar.–May	June–Aug.
No. of occurrences	3	34	11	2	—
Percentage occurrence	1·7	19·4	32·4	16·7	—
Percentage of total volume	0·4	16·4	13·3	0·5	—

(*d*) *Grass and green leaves*

The total green food in each crop was measured volumetrically and then stored. The occurrence and volume of this is shown below. An examination of about 25% of the whole quantity collected showed that the most common leaves were (1) grasses, (2) clovers, (3) buttercups. The grasses include portions of most of the common species listed under seeds and small quantities of cereal leaves—from young corn. The clovers were a fairly even mixture of red and white clovers (*Trifolium pratense*, *T. repens*) and black medick (*Medicago lupulina*). Leaves of the three common buttercups, *Ranunculus repens*, *R. bulbosus* and *R. acris*, occur frequently. Other leaves of common weeds such as *Polygonum aviculare* are found in small quantities. The leaves of cultivated crops such as kale, brussels-sprouts, cabbages and beet are rarely eaten in appreciable quantities.

	Sept.	Oct.–Nov.	Dec.–Feb.	Mar.–May	June–Aug.
No. of occurrences	124	141	29	12	23
Percentage occurrence	70·0	80·5	85·4	100·0	74·2
Percentage of total volume	9·9	26·5	68·0	92·2	14·4

(*e*) *Animal food*

As already stated, animal food is important only during the summer months.

	Sept.	Oct.–Nov.	Dec.–Feb.	Mar.–May	June–Aug.
No. of occurrences	18	9	—	2	22
Percentage occurrence	10·2	5·1	—	16·7	71·0
Percentage of total volume	0·6	0·04	—	0·02	11·8

Of the total volume (19·75 c.c.) of animal food found, 15·22 c.c. consisted of ants and ant pupae. The most common ants were *Myrmica scabrinodis* Nyl. and *Acanthomyops niger* L., but *Myrmica ruginodis* Nyl. and *Acanthomyops flavus* F. also occurred. The following species occur in small quantities only and in few crops.

Coleoptera:

Tachyporus hypnorum F.
Xantholinus linearis Ol.
Sitona lineatus L.
S. sulcifrons Thunb.
S. flavescens Marsh.
S. humeralis Steph.
Sitona sp. indet.
Phytonomus nigrirostris F.
P. punctata F.
Phyllobius pomonae Ol.
P. parvulus Ol.
Cneorrhinus plagiatus Schol.
Amalus haemorrhous Hbst.
Helophorus nubilis F.
Bembidion lampros Hbst.
Pterostichus vulgaris L.
P. madidus F.
Calathus fuscipes Goez.
C. melanocephalus L.
Amara familiaris Duft.
Demetrius atricapillus L.
Ophonus angusticollis J. Mill.
Sermyla halensis L.
Phyllotreta nigripes F.
Dascillus cervinus L.

COLEOPTERA (*cont.*):
Cantharis rustica Fall.
C. rufa L.
Agriotes obscurus L.
A. sputator L.
Coccinella 22-punctata L.
Stilbus testaceus Pz.
Liodes dubia Kug.
ORTHOPTERA:
Chorthippus bicolor Charp.
DERMAPTERA:
Forficula auricularia L.
LEPIDOPTERA:
Adults and Larvae, Spp. indet.
HYMENOPTERA:
Tenthredinidae
Tenthredopsis inornata Cam.
Athalia lineolata Lep.
Cephidae
Larvae, Sp. indet.
Ichneumonoidea
Spp. indet.
Proctotrypoidea
Sp. indet.
Other Hymenoptera
Spp. indet.
DIPTERA:
Tipulidae
Tipula sp.
Limnobius sp.
Chloropidae
Meromyza variegata Mg.
Sp. indet.
Muscidae
Sp. indet.
Tachinidae
Sp. indet.
HEMIPTERA-HOMOPTERA:
Cercopidae
Philaenus lineatus L.
Jassidae
Athysanus communis Sahl.
Sp. indet.
HEMIPTERA-HETEROPTERA:
Lygaeidae
Sp. indet.
Capsidae
Miris laevigatus Fall.
Megaloceraea erratica L.
Lygus sp.
Spp. indet.
Reduvidae
Nabis ferus L.
Nabis major Cost.
Aphididae
Spp. indet.
ARANEIDA:
Spp. indet.
OTHER ANIMALS:
Snail, sp. indet.

(*f*) *Grits*

Apart from sand and soil debris, small pieces of grit of the type normally found in the gizzard occurred in many crops. The following table summarizes the occurrence of these.

	Sept.	Oct.–Nov.	Dec.–Feb.	Mar.–May	June–Aug.	Totals
No. of occurrences	40	43	11	2	6	102
Total no. of grits	99	182	44	6	22	353
Percentage occurrence	22·5	24·6	32·3	16·6	19·4	23·8

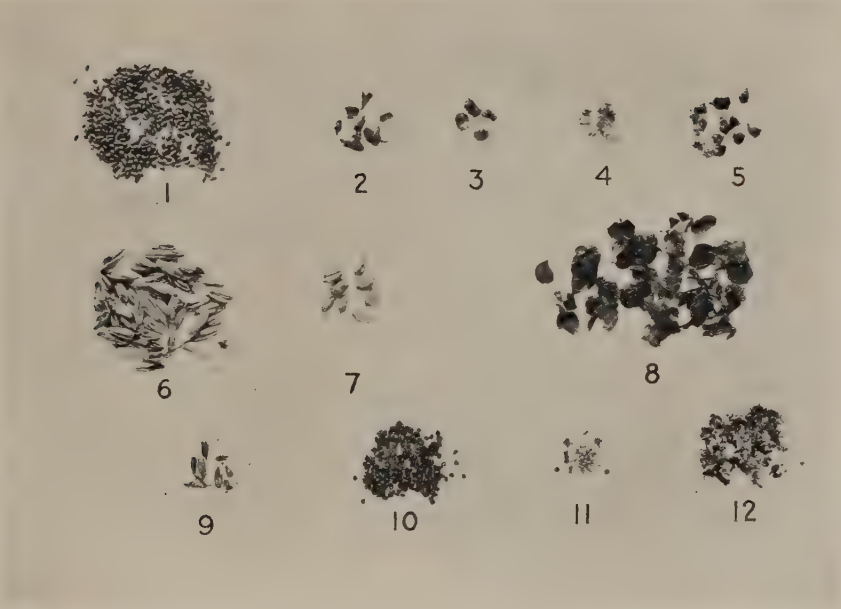
None of the crops examined contained large quantities of grit, the largest number found in one crop being 33.

Food of old and young adults

As it seemed probable that the food of young partridges in the autumn months might differ from that taken by the old birds (their parents), the September figures have been subdivided, but it will be seen that there is no significant difference between old and young.

The food of old and young partridges during September

	Old (62 crops)		Young (82 crops)	
	Vol. (c.c.)	%	Vol. (c.c.)	%
Seeds (weeds, etc.)	22·49	12·7	25·12	10·1
Grain	131·34	74·4	204·58	82·6
Flowers and buds	0·88	0·5	1·00	0·4
Roots	1·70	1·0	0·10	0·04
Grass and leaves	17·87	10·1	16·42	6·6
Animal food	2·19	1·2	0·61	0·2



Phot. 2. Contents of crop of partridge killed in Hampshire, Sept. 8th, 1933. 1. *Galeopsis Ladanum*. 2. *Chrysanthemum segetum* buds. 3. *Papaver* buds. 4. *Anagallis arvensis*. 5. *Papaver* capsules. 6. *Hordeum sativum*. 7. *Triticum*. 8. Clover leaves. 9. *Cerastium vulgatum*. 10. *Silene inflata* with *Lychnis alba*. 11. *Euphorbia exigua*. 12. Débris.

Phot. 3. Contents of crop of partridge killed in Norfolk, Oct. 6th, 1934. 1. Clover and grass. 2. *Polygonum aviculare*. 3. *Hordeum sativum*. 4. *Polygonum Convolvulus*. 5. *Viola tricolor*. 6. *Stellaria media*. 7. *Convolvulus arvensis*. 8. *Anagallis arvensis*. 9. *Atriplex patula*. 10. Unidentified. 11. *Poa annua*.

Quantity of food eaten

During the autumn and winter 1936–7 some hand-reared partridges were kept in a grass pen in front of our laboratory window. These birds were fed continually on seeds and grain, always having an excess available. The amount of grass and green leaves eaten was not measured but, from observation, did not represent a very high proportion of the total food. The quantities of seeds and grain eaten over several periods were carefully measured and worked out as follows:

Month	No. of birds	No. of days	Total food eaten (g.)	Av. per bird per day
October	3	5	327·3	21·8
,,	3	5	370·2	24·6
November	2	6	253·5	21·1
February	2	4	204·9	25·6
,,	2	4	182·4	22·8
March	2	4	225·0	28·1
	Total for 66 bird-days		1563·3	23·7

The heaviest crop from a wild bird examined during September (when natural food would approach nearest to the conditions in our pen) weighed 18·3 g. Assuming that the total food consumption per 24 hours might be between 25 and 30 g. this would mean the equivalent of not more than two fairly full crops per day. Field observation indicates that wild partridges feed intermittently during the day but intensively shortly before dusk. Full crops are often found at roosting time but rarely during the early part of the day. During the winter and spring months, when most of the food is greenstuff, owing to the more bulky nature of grass, etc., the volume eaten would have to be much greater to give the same weight. Table 1 shows that the average volume of crops examined in September was 2·85 c.c., while the volume for December–May averages 6·22 c.c. per crop (these figures, of course, include many crops containing very small quantities of food).

4. Red-legged partridges (*Alectoris rufa*)

The crops of red-legged partridges were collected as opportunities occurred during this investigation. The food found in the 29 crops examined is shown in Table 3. Of these crops, 16 were taken in September and 13 in October and November. If Table 3 is compared with the September–November period in Tables 1 and 2 it will be seen that there is a general similarity in the foods eaten by grey and red-legged partridges. The proportion of roots (28·2%) is noticeably high, but may be due to the fact that most of the red-legs came from Norfolk, where sugar-beet is a common crop. Beech mast (*Fagus sylvaticus*) which occurred in three of the red-leg crops was not found in the grey partridge. Two species of *Polygonum* are commonly found in both.

Table 3. *The contents of the crops of* 29 *red-legged partridges* (Alectoris rufa), *total volume* 109·72 c.c.

	No. of occurrences	Total vol. (c.c.)	% vol.	% occurrence
Grass, clover and leaves	22	17·50	16·0	76·0
Flowers and buds	2	0·20	0·2	6·9
Roots (sugar-beet, etc.)	6	30·90	28·2	20·7
Animal food	2	0·01·	0·01	6·9
Seeds and grain:				
Knotgrass, *Polygonum aviculare*	15	18·33	16·7	51·7
Barley, *Hordeum sativum*	6	14·00	12·8	20·7
Wheat, *Triticum*	7	10·26	9·4	24·1
Beech mast, *Fagus sylvaticus*	3	6·40	5·8	10·3
Oats, *Avena sativa*	3	5·71	5·2	10·3
Bindweed, *Polygonum Convolvulus*	12	1·62	1·5	41·4
Spurge, *Euphorbia exigua*	7	1·25	1·1	24·1
Orache, *Atriplex patula*	1	0·95	0·9	3·4
Charlock, *Brassica arvensis*	6	0·57	0·5	20·7
Wild Pansy, *Viola tricolor*	5	0·29	0·3	17·2
Other seeds in small quantities*	—	1·73	1·6	—
Total vol. of seeds ..	—	31·14	28·4	—
Total vol. of grain	—	29·97	27·3	—

* Scarlet pimpernel, *Anagallis arvensis*; chickweeds, *Stellaria media* and *Cerastium vulgatum*; forget-me-not, *Myosotis arvensis*; campions, *Silene inflata* and *Lychnis alba*; hemp-nettle, *Galeopsis Ladanum*; viper's bugloss, *Echium vulgare*; hawk's beard, *Crepis virens*; toadflax, *Linaria Elatine*; hawkbits, *Leontodon hispidus* and *L. autumnalis*; goosefoot, *Chenopodium album*; shepherd's purse, *Capsella Bursa-pastoris*; wild radish, *Raphanus Raphanistrum*; brome grass, *Bromus arvensis*; Italian ryegrass, *Lolium italicum*; meadow grass, *Poa annua*.

5. Partridge food and game management

Four of the important factors limiting or influencing the density of partridges on any area are: (1) food, (2) nesting cover, (3) summer cover, and shelter for the very young birds, and (4) predators. Game preservers seek to maintain the highest possible density by making the environment favourable for partridges and destroying predatory animals. In practice, the work of the partridge keeper has to be concentrated mainly on the destruction of predators and the protection of the partridge from disturbances of many kinds, and he has little chance to make significant changes in the available food supply and cover.

In naturally favourable environments "vermin" destruction and protection have allowed the partridge population to reach very high densities at certain times, but there is a limit to the carrying capacity of any area beyond which the population cannot be forced without changing one or more of the first three factors mentioned above. The density limit is undoubtedly controlled, not by one of these factors alone but by the correct balance between them.

The results of this study of the foods actually eaten by wild partridges on preserved estates throughout the year indicate certain possibilities in the improvement of the food supply. From Fig. 1 it is clear that whenever seeds and grain are available in quantity the partridges show a definite preference for them. The very large proportion of green food eaten during the winter and

spring months is almost certainly due to the fact that there is little else available rather than to any preference on the part of the birds.

This conclusion is supported by observations of the behaviour of adult partridges kept throughout the year in a wired enclosure, and also by winter feeding trials carried out on the Imperial Chemical Industries research estate at Knebworth, where wild partridges regularly fed at observed artificial feeding places.

During this period there is invariably a heavy loss of stock on the preserved estates (**3**) partly due to movement at the pairing time and partly to mortality. This winter "wastage" of the adult birds left after shooting is one of the most serious losses facing game preservers since it so greatly reduces the breeding stock on which the next season's crop depends. Although much of the movement at pairing time is probably due to territorial behaviour among the mating birds, it is clear that certain favourable environments have a higher carrying capacity than others, and the nature of the available winter food may be presumed to be an important factor in any environment.

For many years keepers on some estates have fed their partridges during the winter with grain and seeds, but in most cases such feeding is carried on only in hard weather for limited periods, usually between December and March. It is obvious that if artificial feeding is to increase the carrying capacity of any area it must be a permanent factor in the environment, and Fig. 1 suggests that the seasonal shortage of grain and seed food is continuous from December to May. To be effective, winter feeding should be carried on for the whole of that period.[1] It is probable that winter feeding, as well as influencing the carrying capacity of the land, may increase the resistance of the birds to bad weather conditions and diseases such as pneumonia, from which there is severe mortality during some winters. A mixture of seeds and green leaves is probably a more correctly balanced diet than greenstuff alone. Since the larvae of *Trichostrongylus tenuis* (a nematode worm causing widespread mortality among adult partridges (**4**)) are attached to grasses, clovers, etc., winter feeding may be expected to reduce the rate of infection by decreasing the amount of green food eaten and consequently the number of larvae ingested.

The provision of special feeding grounds for game birds in winter by sowing patches or strips of late seeding species has received little attention in this country, although it is practised extensively in America (**2**, **5**, **6**, **7**). Buckwheat is commonly sown for this purpose, but more with the object of holding pheasants than partridges; in any case its seed supply is exhausted too early in the winter to fulfil the requirements of partridges. But the deliberate cultivation of plants generally treated as noxious weeds is not regarded favourably by farmers.

[1] A leaflet (Advisory Leaflet No. 14), giving detailed advice on methods of supplying food for partridges in winter, has been published by Imperial Chemical Industries, Millbank, London.

6. Summary

The contents of the crops taken from 429 adult grey partridges (*Perdix perdix*) and 29 red-legged partridges (*Alectoris rufa*) have been analysed. The food eaten by the common grey partridge changes seasonally, being composed largely of seeds and grain in autumn and nearly all grass and green leaves in late winter and spring. Sugar-beet pulp is eaten during winter. Flowers and buds form an important part of the food during summer. Animal food (mostly ants and their pupae) occurs in significant quantities only during the summer months. The food of the red-legged partridge is similar.

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A CENSUS OF THE ECTOPARASITES OF SOME CEYLON BATS

By GORDON B. THOMPSON

This paper contains the results of an attempt to take a census of the ectoparasites of six species of bats occurring in Ceylon. I am indebted to Capt. W. W. A. Phillips for the material and should like to take this opportunity of expressing my gratitude to him for the careful way in which he has carried out his part of the task. Altogether 18 specimens of bats have been examined and as far as possible Capt. Phillips has collected every parasite off each host specimen. I am fully aware that, in order to enable one to draw any conclusions from the results obtained, considerably more than 18 bats should be examined, but I feel that the few results which I am able to present here may serve to throw some light on an aspect of parasitism which has been little studied.

No complete census of more than a single host species of bat appears to have been published hitherto. Scott (1908), in his account of the variation which occurs in the Nycteribiid *Cyclopodia sykesi* Westwood, records that 57 males and 43 females of this parasite, together with numerous mites of the genus *Leiognathus*, were obtained from 11 male specimens of *Pteropus giganteus giganteus* (Brünnich) (the common flying fox) at Barberyn Island, off the west coast of Ceylon. Muir (1912) gives a rough account of the number of specimens of parasitic Diptera which he found at Amboina on just over 100 bats representing four species. Phillips (1924) records the comparative abundance of the various species of parasites occurring on Ceylon bats. Hase (1931) draws attention to the fact that very few data are available concerning the numbers of parasites occurring on bats and records that normally only two or three specimens of Nycteribiidae were found on *Myotis* sp. in Venezuela. Smith (1934) gives an account of observations on the habits and host relationships of various species of Nycteribiidae and Streblidae occurring on two species of bats: *Tadarida mexicana* (Sausure) and *Corynorhinus rafinesquii pallescens* (Miller). He mentions the numbers of parasites per host in some cases. The points of interest mentioned by Smith as possibly having some influence on the numbers of bat-flies occurring on a particular host are the length of the hair, the size of the ears and the habits of the host, i.e. whether solitary or gregarious.

In two recent papers (Thompson, 1935, 1936) I have recorded the total number of specimens of parasites collected off some examples of British bats. A thorough examination of the literature will probably reveal numerous instances where authors have mentioned the total number of Nycteribiidae or Streblidae, or of both groups, found on single hosts, but time does not

permit me to go further into this matter. A very complete bibliography is given by Hase (1931).

Bats are excellent hosts from the point of view of the parasitologist in view of the fact that so many species of parasites representing numerous groups have been recorded from them. The parasites recorded contain representatives of the following groups of Arthropoda: Hemiptera-Heteroptera; Cimicidae, Polyctenidae (bat-bugs); Diptera: Nycteribiidae, Streblidae (bat-flies); Siphonaptera (fleas); Ixodoidea (ticks); Parasitoidea, Demodicoidea, etc. (bat-mites). Arixeniidae, a family of Dermaptera, have been recorded as parasites of bats but I am of the opinion that their occurrence on bats is purely accidental. From the 18 specimens of bats included in this paper the following groups of parasites were obtained: Nycteribiidae, Streblidae, Siphonaptera, and Spinturnicinae.

In Table 1 the number of specimens of each sex of the larger parasites, i.e. Nycteribiidae, Streblidae and Siphonaptera, is given, whereas only the total number of specimens of the mites is given. Only a single specimen of a flea was obtained from *Rousettus seminudus*—fleas seem to be particularly rare on the bats themselves in the tropics. I have, however, seen large series bred from the excreta of bats from a cave in Java.

The following notes on the position of the parasites on their hosts are of interest. It seems a great pity that more data are not available with regard to this matter, as I feel sure it is of great importance in cases where two or more closely related species of parasites occur on a single host specimen. Nycteribiidae seem to occur for the most part among the fur of the neck and breast. Streblidae are to be found on the wing membranes as well as on the body among the fur. Mites (Spinturnicinae, etc.) seem to be confined almost entirely to the underside of the wing membrane.

Table 2, which gives some particulars of the hosts themselves, is of interest when considered in conjunction with the census.

Table 2

Species of bat (all small gregarious species)	Length of hair		Distribution		Comparative frequency of parasites	
	Long	Short	Common	Rare	Free	Heavy
Scotophilus wroughtoni	—	×	×	—	—	×
Pipistrellus coromandra	—	×	×	—	×	—
Miniopterus fuliginosus	×	—	×	—	—	×
Saccolaimus saccolaimus	—	×	×	—	×	—
Rhinolophus rouxi rouxi	—	×	×	—	×	—
Rousettus seminudus	—	×	—	×	—	×

As so little is known regarding the life histories of bat parasites it is impossible to say whether there is any seasonal variation in the number of parasites per host. For information regarding the life histories of Nycteribiidae see papers by Hase (1931), Rodhain & Bequaert (1916), Scott (1917, 1934), Ferris (1930) and Muir (1912).

Table 1

Species of bat	No. of specimens of bat examined	Diptera-Nycteribiidae																D	
		Penicillidia bathybothyra Speiser		*Penicillidia Jenynsi* var. *indica* Scott		*Nycteribia (Listropodia) allotopa* Speiser		*Nycteribia (Listropodia)* sp.		*Nycteribia (Acrocholidia) phillipsi* Scott		*Cyclopodia (Paracyclopodia) royleï* (Westwood)		*Eucampipodia [illegible]* (Kolenati)		*Tripselia amiculata* (Speiser)		*Raymondia pagodarum* (Speiser)	
		♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Scotophilus wroughtoni Thos. (Wroughton's bat)	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
	1	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
	1	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
Pipistrellus coromandra Gray (Coromandel Pipistrel)	1 ♂	.	.	.	.	.	.	.	.	.	.	4	2	.	.	.	.	.	.	.	.
	1	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Miniopterus fuliginosus Hodgs. (long-winged bat)	1 ♂	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 ♂♂	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
	1 ♂	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 ♂	.	.	.	3	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Saccolaimus saccolaimus Temm. (pouch-bearing sheath-tailed bat)	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.
	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhinolophus rouxi rouxi Temm. (Rufous horse-shoe bat)	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rousettus seminudus Kel. (Ceylon fruit-eating bat)	1 ♂	.	.	.	.	.	.	.	.	.	.	.	.	4	1	.	.	.	.	.	.
	1 ♀	.	.	.	.	.	.	.	.	.	.	.	.	5	3	.	.	.	.	.	.
	1 ♀	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	1 ♂	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.

* *Spinturnix acuminatus* Koch. † One specimen of Nycteribiidae escaped.

N.P. = Northern Province; P.E. = Eastern Pro

ptera-Streblidae				Acarina			Total no. of parasites				
♀ *Nycteribosca amboinensis* (Rondani)	♂ *Nycteribosca amboinensis* (Rondani)	♀ *Nycteribosca modesta* Jobling	♂ *Nycteribosca modesta* Jobling	Spinturnicinae	Undet. gen. et spp.	Siphonaptera	Nycteribiidae	Streblidae	Acarina	Siphonaptera	Locality, etc. of host
.	.	.	.	4*	.	.	2	.	4	.	N.P., Kankesanturai, 24 Dec. 1934
.	.	.	.	.	.	.	2	.	.	.	N.P., nr Jaffna, Aralia, 25 Dec. 1934
.	.	.	.	.	.	.	2	.	.	.	E.P., Kantalia, alt. 250 ft., 25 May 1935
.	.	.	.	2*	.	.	6	.	2	.	E.P., nr Kokkalai, Palmoddai, 13 June 1936
.	.	.	.	.	.	.	3	.	.	.	N.P., Kankesanturai, 24 Dec. 1934
2	.	.	.	.	.	.	1	2	.	.	C.P., Gammaduwa, Mousakande, alt. 3400 ft., 21 Mar. 1935
1	1	.	.	.	.	.	3	2	.	.	C.P., Gammaduwa, Mousakande, alt. 3400 ft., 9 Apr. 1935
1	.	.	.	.	.	.	1	1	.	.	C.P., Gammaduwa, Mousakande, alt., 3400 ft., 9 Apr. 1935
.	1	.	.	.	.	.	6	1	.	.	C.P., Gammaduwa, Mousakande, alt., 3350 ft., 8 Feb. 1935
.	.	.	.	.	.	.	3	.	.	.	N.C.P., Kikirawa, alt., 430 ft., 3 Feb. 1934
.	.	.	.	1	.	.	2	.	1	.	C.P., Gammaduwa, Mousakande, alt., 3350 ft., 5 Jan. 1935
.	.	.	.	.	.	.	.	.	.	.	C.P., Gammaduwa, Mousakande, alt., 3350 ft., 6 Feb. 1935
.	.	2	2	.	.	.	1	4	.	.	C.P., Gammaduwa, Mousakande, alt., 3300 ft., 28 June 1935
.	.	.	.	.	5	.	1†	.	5	.	C.P., Gammaduwa, Mousakande, in cave, alt., 3300 ft., 24 July 1935
.	.	.	.	.	.	.	5	.	.	.	C.P., Matula Distr., nr Rattota, in cave, alt. 1500 ft., 14 Aug. 1935
.	.	.	.	.	.	.	8	.	.	.	Ditto
.	.	.	.	?1	3	1♀‡	.	.	4	1	Ditto
.	.	.	.	.	2	.	1	.	2	.	Ditto

‡ *Thaumopsylla breviceps* Rothschild. § Females with young.

vince; C.P. = Central Province.

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SUMMARY

A complete census of the ectoparasites from 18 specimens of Ceylon bats belonging to six species is recorded. References are given to the still limited literature on bat parasite populations, and the position of parasites on the body of the host is discussed.

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BEHAVIOUR OF THE RED-LEGGED EARTH MITE, *HALOTYDEUS DESTRUCTOR*, IN RELATION TO ENVIRONMENTAL CONDITIONS

By M. E. SOLOMON

(*With* 10 *Figures in the Text*)

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1. Introduction

Halotydeus destructor (Tucker) (Acarina, Family Penthaleidae) feeds upon many pasture and garden plants in Australia and South Africa. The body is black, about 1 mm. long in the adult; near the anterior end it bears three ocelli,

a median one and a lateral pair. The eight legs are red in colour and about as long as the body. The mites die on the approach of summer, only the eggs surviving. Accounts of the biology of the mite have been given by Tucker (1925) and Swan (1934).

The earth mite is very active, the greater part of its life being spent in running about on the ground or on plants. If kept in slightly unfavourable conditions, it will run hither and thither continuously for days on end until it dies (cf. Tucker, 1925). Thus running is the basis of most of the other activities, and the more specific responses which are considered in this paper are mostly modifications of this generalized response.

The tests carried out in the laboratory followed on observations and sometimes experiments in the field. The method most frequently used in the laboratory was to enclose the mite, or group of mites, in a piece of glass tubing about 1 ft. in length, plugged at either end with cotton-wool or glass rod. By this means it was usually easy to determine whether the mites were attracted or repelled by a given stimulus, or were indifferent to it. Each test was performed with at least three different groups of mites, and as many as possible were checked from general observations made during 12 months' work with the mites in field and laboratory.

2. Reactions to light

It is difficult to discover the mites' reactions to light simply by observation in the field. They tend to avoid strong sunlight, particularly in spring, when it is often hot enough to kill them; but if the sunlight is mild, the mites are to be seen feeding on the upper surfaces of the leaves, and running on the open sand. These facts could be explained simply as resulting from a preference for bright light, providing that the intensity (or perhaps heat) does not exceed a certain value. But this explanation would not cover the further fact that when the sun is hidden behind clouds or screened off by buildings, the mites show a preference for fairly dim light. In fact, as shown below, there is one set of reactions in relation to sources of light, and another set in relation to variations in light intensity.

(*a*) *Reactions to sources of light*

In the laboratory, adult, nymphal and larval mites enclosed in long glass tubes plugged at either end showed a definite positive phototropism. That is, they moved towards a well-defined source of light, such as a window or an electric light. However, the reaction was not absolute. On reaching the plug at the end of the tube, a mite would turn and make a longer or shorter journey away from the direction of the source before turning again. Sometimes it would turn back (away from the source) before reaching the plug. But on the whole it spent more time in the end near the source, less in the other parts. This was demonstrated in many cases by tracing on paper the movements of a

mite in a glass tube (see Fig. 1). Since glass does not transmit ultra-violet radiations, the phototropism was tested with a silica tube, and by leaving the mites free to run on flat surfaces near windows, etc. Also some strong lights were tried, including the water-cooled beam from an electric projection lantern (intensity of beam about 3000–4000 foot-candles) and a mercury vapour lamp. In all cases a positive phototropism was observed. Moreover, the reaction occurred at all humidities, and at all temperatures at which the mites were capable of sustained activity. When temperature or humidity was unfavourable to the mites they were more restless and the response was readier. Groups of mites that had undergone desiccation almost to the point of death, and also mites that had been kept for days under very moist conditions were still positively phototropic.

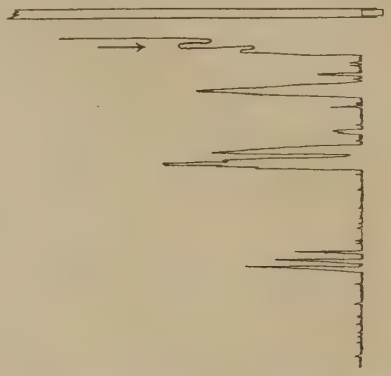


Fig. 1. Chart of movements of *Halotydeus destructor* in a glass tube which is pointed towards the lighted window. The tube is closed at each end by a smooth glass stopper. Only 16 cm. of the tube is shown in the diagram.

In sunlight, however, the positive phototropism was no longer clearly shown. If a number of mites were released in the field in direct sunlight, they moved off in all directions. When those mites which moved towards the sun were collected again, and released together, usually they also scattered in all directions. In some cases it was found possible to separate out a group of mites which moved consistently towards the sun, but generally the movement of the mites in sunlight seemed to be directed at random, without reference to the position of the sun. The same result was obtained when the sunlight was cooled by means of an intercepting water-bath; as, for example, in one case in which the sun temperature was 35° C., the shade temperature 23° C., and the temperature behind the water-bath 26° C. Hence it seems that the high intensity must be responsible for the failure of the phototropic reaction, and not the heat of the sun's rays.

In one group of experiments, it was found as usual that the mites moved at random when on the ground in the bright sunlight. Then about 30 mites were

put into a glass tube 34 cm. long and 1·5 cm. wide, which was laid on the ground with one end pointing towards the sun; 10 mites went to the end nearer the sun, and remained in that region, while about 20 mites showed a preference for the opposite end. A few mites wandered between the two groups, which however remained fairly distinct and readily crossed over to opposite ends of the tube when it was reversed. Then 13 mites were taken from the negatively heliotropic group, and transferred to a smaller glass tube 0·5 cm. wide, which was laid down horizontally with one end pointing towards the sun. Seven mites were attracted to this end. (The greater curvature of the smaller tube caused it to reflect more light, so that the intensity within was less.) When they were returned to the wider tube, only 3 were positively heliotropic. Finally, they were put back into the smaller tube, when 9 were positively heliotropic.

These results suggested that the positive heliotropism was being inhibited by the intensity either of the direct sunlight, or of the light from the sky and surrounding objects. To test the latter possibility a box was placed over a tube of mites as in Fig. 3, so as to exclude most of the skylight, but not the direct sunlight. After a number of repetitions it was concluded that this had no effect in increasing the proportion of mites which showed positive heliotropism.

The phototropic activity may persist for a short period after the passing of the stimulus which evoked it. Thus, when mites were enclosed in a long plugged tube, one end of which pointed towards, but a little below, the source of light (Fig. 4) they moved from the darker end B towards the light. But instead of stopping at D, the last point from which the source of light was visible, the mites continued into the region A where the view of the source was cut off by an opaque screen. They remained in this shaded part for a short period and then retreated to the region D. (In one of several repetitions of this experiment, there was a fairly general avoidance of end A from the beginning, the mites concentrating on the region D.)

(*b*) *Reactions to light intensity*

When there is no source of light visible, the mites show a selective activity in relation to light intensity. They avoid darkness, on the one hand, and very bright light, on the other. In a number of experiments, mites were enclosed in a long glass tube which was placed horizontally and perpendicular to the light rays from a window. If a part of the tube was covered outside with black paper, the mites usually avoided this darkened section altogether, though occasionally a mite would wander into it for a brief period. If a section of the tube was in sunlight, the majority of the mites avoided this also.

For example, 50 mites were enclosed in a glass tube 16 cm. long; half of the length of the tube was in direct sunlight, the other half was shaded by an opaque screen; counts made at intervals showed that there were, on an average, three times as many mites in the shaded half of the tube as in the sunlit half. Mites in a glass or silica tube also tended to avoid the beam of a projection

lantern (although when the tube was turned parallel to the beam the mites were positively phototropic), and gathered in the subdued light on either side of the bright region. In this case the beam travelled first through 13 cm. of cold water, so that it was cooled and could not be felt on the hand. Its intensity was about 1500 foot-candles. Hence the avoiding reaction seems to be truly a response to light, not (in this case) to heat. Further evidence of this is given later.

Mites were put into a glass tube which was marked off into three equal lengths, A, B and C, and placed parallel to a window (see Fig. 5). Section C was open to the bright sunlight, section A was shaded by an opaque screen,

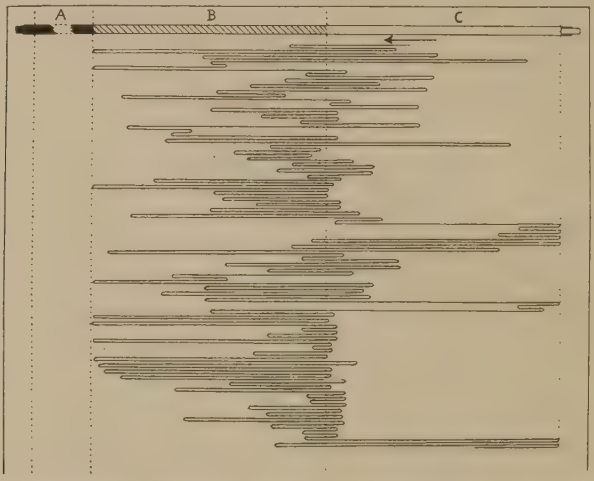
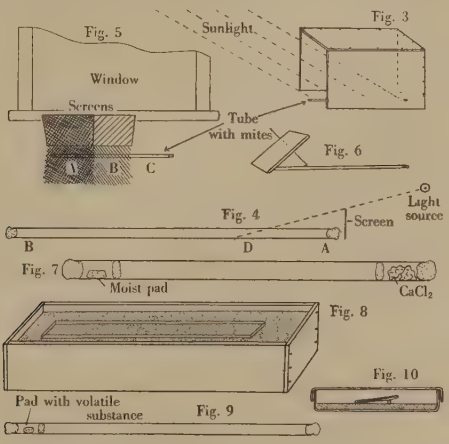


Fig. 2. Chart of movements of *Halotydeus destructor* in a glass tube closed at each end by a smooth glass stopper. The tube is 30 cm. long: the 10 cm. section C is in sunlight, the middle 10 cm. (B) in room daylight, while the 10 cm. section A (part omitted) is covered with black paper. Temperatures: B, 24·5° C.; C, 28° C.

while the middle section B was shaded by white paper, oiled to render it translucent. Most of the mites gathered near the median end of the screened section A, as if they found the complete shade too dark, and the middle section too light. When the sun was obscured behind dense clouds, the mites scattered more evenly along the tube, and there was no significant difference between the numbers in the two lighter sections, B and C.

In Fig. 2 the movements of a single adult mite in relation to sunlight, room daylight and darkness are recorded. There was a complete avoidance of darkness. Obviously section B was nearest to the optimum illumination, but was probably a little below it, for there was a continual tendency to pass into section C, which however proved too bright (the somewhat higher temperature in C may have been an additional factor).

Another example of the selection of a light intensity less than that of normal daylight is provided by the following test, which was repeated many times. A group of mites was placed near the overhanging side of a board which projected for 10 cm. at an angle from the ground: most of the mites ran in under the board, where the shade was deeper. (An apparent reversal of this result was obtained when one end of a tube containing mites was inserted under the board (Fig. 6): the mites avoided the shaded part. But when they were tipped out on the sand they went in under the board. The glass tube used was 30 cm. long, 0·5 cm. wide, and the same result was obtained with a silica tube 0·65 cm. wide. The reversal was presumably caused by a reduction in light intensity, due to reflection from the walls of the tube, so that the illumination in the part of the



Figs. 3–10. Arrangement of apparatus in some of the experiments. Description in text.

tube under the board was less than the minimum which is attractive to the mites; or it may have been due to the relatively bright section of the tube appearing to the mites as an attractive source of light.)

In the field mites are often observed to avoid the sunlight when it is strong. For example, they prefer to feed on the shaded sides of leaves. However, in favourable weather they crowd on the exposed parts of the plants towards sunset, or when the sun is obscured behind clouds. Under these conditions it seems that the light is not strong enough to repel them from favourable feeding sites.

Under some conditions, even when the sunlight is bright, no clear avoiding reaction is shown. For example, when mites are running on the soil across patches of alternate shade and sunlight, they often seem to move quite independently of light conditions.

A reaction to a sudden change in light intensity was sometimes observed. For example, in certain experiments (§ 4(*b*)) the mites came to rest in groups on damp sand. If, while the mites were in this condition, a sudden change from subdued to bright illumination was made, the mites scattered and ran about for a few seconds, then usually settled down again into one or more groups as before. The same reaction may be observed at night in the field by directing the light of a torch on to groups of mites under plants, or sometimes in daylight by gently raising a leaf under the shadow of which mites are resting.

3. Reactions to heat

The most obvious effect of heat on the mites' behaviour is to regulate the rate of locomotion. At higher temperatures, the mites run more rapidly and turn more often. Conversely, a fall in temperature causes a decrease in activity. On a cold night, or early in the morning, mites may be seen to be immobile on the leaves, as if frozen; however, their power of movement is soon restored as the temperature rises.

It was suggested in the previous section that the avoidance of strong sunlight by the mites is partly a heat-reaction. Laboratory experiments showed that the mites avoid high temperatures. When one end of a glass tube containing mites was placed close to a red-hot electric coil, the mites at first advanced towards this end, because of the relative brightness of the coil in the darkened room. But about a point B they began to move more rapidly; if headed towards the hot end they ran more and more quickly, but soon turned, and since they turned less often as the temperature became lower, they gradually moved back from B, and grouped themselves along the tube on the cooler side of this point. The temperature at B, judged very roughly by holding a thermometer beside the tube, was 40–50° C. (This trial-and-error type of behaviour, in which the response to unfavourable conditions was an increase in activity, was also noted in connexion with the humidity reactions (§ 4(*b*)). However, if there is a sudden transition to hot conditions, such as a mite experiences in passing from the shade into very hot sunlight, it turns back almost immediately.)

An analogous experiment was designed to discover whether the mites have any cold-avoiding reaction. One end of the tube was immersed in a bath of ice-water. This cold end was pointed towards the lighted window, so that the mites would move towards it. On arriving at the point where the tube entered the cold bath, most of the mites stopped, or wandered to and fro in this region. A few went on through the cold section, with greatly reduced speed. The temperature of the cold bath was 4·5° C., while the rest of the tube was at 20° C.

To test the reaction of the mites to a temperature gradient, a long trough containing water was packed with cloth to impede circulation; one end of the trough was heated; the other was supplied with a continuous flow of cold water. The glass tube containing mites was suitably plugged, and immersed in the water. (This apparatus was modelled on that described by Agar, 1927.) Three

gradients were tried, namely, 9·5–14·5, 23–30, 26–33° C. In the first case no definite preference could be detected. In the last two cases there was at first a preference for the cooler end; but this reaction became less clear after a time and was not evident when the tube was reversed in the bath.

It appears, therefore, that the mites avoid extremes of temperature, but between these limits their selective activity is not marked.

4. Reactions to moisture

(*a*) *Atmospheric moisture*

Mites were put into a glass tube 25 cm. long and 1·3 cm. wide, and separated by loose plugs of cotton-wool from dry calcium chloride at one end and from a moist cotton-wool pad at the other (Fig. 7). From 10 to 30 mites were used in each of six experiments. In each case the tube was reversed occasionally to correct for any slight unevenness of lighting. In two of these experiments no preference for one end or the other could be detected. In two others there appeared to be preference for the moist end, about two-thirds of the mites concentrating there. But in the other two experiments there appeared to be a preference for the dry end. One of the experiments that yielded a neutral result was performed with mites which had been subjected to desiccation in a dry calcium chloride tube for 5 hours, until some were dead. In the others, the mites used had been collected in the field and then kept on water for several hours. These results indicate that the mites have no strongly developed selective behaviour in relation to atmospheric humidity.

Further experiments of different design were carried out to test this point, including some in which water vapour was blown in at one end of the tube, and others in which streams of dry and of saturated air were directed at mites wandering on a flat surface, but as they yielded results similar to the above, it seems unnecessary to describe them.

But atmospheric moisture affects the rate of evaporation from the mites' bodies and so affects their behaviour indirectly. For it has been found in the course of another series of experiments (Solomon, 1937) that the mites soon become restless in an atmosphere of low humidity, whereas in air of high humidity they tend to come to rest (cf. § 9(*b*)).

(*b*) *Soil moisture*

A box was filled with air-dry sand on which an area, 30 cm. long by 6 cm. wide, was enclosed by vertical glass walls about 1·5 cm. high (Fig. 8). The upper part of the glass wall was coated with vaseline inside to prevent the mites escaping. One end of this enclosed strip of sand was copiously watered, until a damp area extended about half-way along the strip, the remaining half being dry. About 25 mites were distributed along the enclosure. After 15 min. most of the mites had gone to the wetter end of the wet sand, only three remaining

on the dry sand. Although the lighting was fairly even, the box was turned about but the reversal caused no evident change in the distribution of the mites. This experiment was repeated several times. In every case at least 75% (usually more) of the mites chose the wet sand, and most of these chose the wettest part (i.e. the end) of the wet section. The same result was obtained when the box was placed outside in the winter sunlight, also when the box was kept in darkness for half an hour, or overnight.

It was noticeable during these experiments that while the mites on the dry sand were usually restless, running about continuously, those on the wet sand tended to come to rest, most frequently in small crowds at the corners of the enclosure or in depressions in the sand.

It may be concluded that the mites detect and react to the moisture content of the soil: they tend to be restless and active while on dry soil, but become less active on wet soil, with a tendency to come to rest for long periods. The resulting selective activity appears to be of a special trial-and-error type, similar to that described in connection with the heat-avoiding reaction (section 3).

(*c*) *Free water*

The mites are very difficult to wet, and can live for days on the surface film of water. But free water is usually avoided. For example, as is easily shown in the laboratory, the mites turn aside from droplets of water on glass or wood. This is probably a reaction to the physical forces of surface tension. In rainy weather the mites' avoidance of wet conditions causes them to retreat under plants, sometimes under small pieces of wood or stone, and causes them to avoid any except the fairly protected (and therefore dry) parts of the plants. Similarly, when there is a dew on the upper surfaces of the leaves, feeding mites are confined to the drier under-surfaces.

5. Reactions to gravity

Close observation in the field failed to disclose any definite reaction to gravity. In the laboratory, single mites, and also groups of mites (including nymphs and larvae) were enclosed in vertical glass tubes, and their position in the tube observed at intervals. In some cases their movements were continuously traced on paper. When the tubes were not kept in darkness, care was taken to ensure even lighting. No geotropic reaction was found. Apparently the mites move about independently of gravity, as has been observed with certain ants (Russell, 1934). They run about quite readily on the under side of a horizontal glass sheet.

There is apparently an exception to the above general rule, in that the mites prefer the under side of a horizontal surface for oviposition. This seems to be a response to gravity. It may be concluded therefore that the mites are able to detect gravitational stimuli, but generally do not respond to them with any observable modification of behaviour.

6. Tactile reactions

The tactile sense is important. The forelegs, which are somewhat longer than the other legs, are extensively used as tactile organs, as noted by Tucker (1925). They are held out in front of the body and, except when the mite is at rest, they beat continuously on the substratum and surrounding objects. Their action thus resembles that of the antennae of many insects. The forelegs of the larvae, which have only three pairs of legs, are used in the same manner. (In various other species of mites, notably in those of the family Linopodidae, the forelegs are sensory in function and are considerably modified for this purpose, being several times as long as the other legs, and similar to antennae in action and position.) The mouthparts are also frequently applied to the substratum, and the palps and perhaps the other parts are used as tactile organs.

Various substances were put into glass tubes containing mites in order to find whether the mites would prefer to remain on these rather than on the glass surface. Dry sand, paper and collodion film were tested in this way, but no preference was shown for any of these: on the other hand, the mites did not avoid them. Two viscous substances, namely vaseline and liquid paraffin, were found to repel the mites. As there is no repulsion until the mites come into contact with the substances, both of which are chemically inert, it seems clear that the effect is a physical one and not chemical.

The habit of gathering together in clusters, which is described in § 9(*b*), seems to be a reaction to tactile stimuli, the mites being specially responsive to the touch of each others' bodies. Sometimes they show a preference for crevices or places where contact with two or three different surfaces is possible. For example, mites kept in a Petri dish tend to gather in the crevice where the two halves of the dish meet. A similar tendency in mites that are laying eggs is recorded in § 9(*d*) (3).

Vibration

Mites in the field respond to sudden vibrations of the substratum by running rapidly about for a short period. For example, crowds of mites feeding on leaves can be made to scatter by a slight jar on the plant; a smart tap will cause many to lose their footing and fall to the ground. It is almost certainly for these reasons that mites are not found on the upper parts of plants on windy days. Groups of mites at rest on the ground are sometimes disturbed and caused to scatter by the vibration due to the walking of the observer. Mites that are already restless may be caused to run more rapidly by sudden vibrations. Similar responses are observed in the laboratory. In addition, mites that are at first too sluggish to respond to a weak light stimulus may be induced to show the usual positive phototropism by a tap on the tube or other receptacle with which they are in contact.

Wind direction

In the field, there appears to be no marked anemotropic reaction. Unless the mites are swept along by the force of the wind their movements seem to be independent of its direction. The same indifference to wind direction was found in the laboratory, with mites in tubes through which air was flowing, and also with mites on an open surface, when an air stream was directed on to them.

7. Gustatory reactions

The fact that the mites possess a well-developed gustatory sense was clearly proved in laboratory experiments. For example, mites were kept in a Petri dish on damp filter paper; one small area of the paper was moistened in addition with sugar (sucrose) solution. The mites gathered about this area and kept their mouthparts applied to the paper as if feeding. Tests showed that the response was not due to extra moisture in this region. Furthermore, experiments of the type described in § 8 showed that the mites were unable to detect sugar solution from a distance. Another proof of the attractiveness of sugar was provided by giving the mites two dry pieces of collodion film, one of which had previously been soaked in sugar solution. A few mites wandered over the untreated collodion, applied their mouthparts occasionally without settling down, and soon left it. But almost all of those which came in contact with the sweetened collodion applied their mouthparts and remained upon it, apparently feeding. Both of the above experiments were repeated a number of times under different conditions.

To test the relative attractiveness of some common sugars, an experiment was performed with six Petri dishes each containing about 20 mites. A small dry sample of the sugar to be tested was placed at the centre of a moist filter-paper in the bottom of the dish. After a few minutes, a proportion of the mites in some of the dishes had gathered about the sugar and seemed to be feeding on the solution. It was found that the sucrose attracted the greatest proportion of mites (about 50%); maltose and fructose were a little less attractive, glucose considerably less, and lactose and galactose not at all. The experiment was repeated twice.

It appears that sweetness as determined by the human taste organs is not the attractive feature in this experiment, because the sugars arranged as above, in order of attractiveness, are not in order of sweetness (even when solubility in water is taken into account). Furthermore, it was found that a solution of glycerol was not in the least attractive to the mites, in spite of its sweetness. Other substances to which they were found to be indifferent were malic acid, amino-acetic acid, starch and egg albumen.

Probably a thorough study of the chemical basis of the taste reactions would throw light on the plant host preferences of the mites.

8. Olfactory reactions

Laboratory experiments showed that the mites were able to detect and react to volatile substances without coming into mechanical contact with them. About 100 mites were enclosed in a long glass tube plugged at each end with cotton-wool. A small pad of cotton-wool was moistened with the substance to be tested and placed inside the tube near one end, being separated from the mites by a further loose plug of cotton-wool (Fig. 9). The end of the tube containing the test substance was pointed towards the window, so that the mites would move phototropically towards that end of the tube.

From certain substances there was an evident repulsion, strong enough, in some cases, to prevent most of the mites from approaching nearer than 6–7 cm. to the substance. The following were found to be repellent: phenol, xylene, oil of turpentine, dilute ammonia, clove oil, amyl acetate. Glycerol and also linseed oil were tested but the mites showed no reaction to them. (No definite repulsion was observed with 70% ethyl alcohol, but nevertheless the alcohol vapour proved quickly fatal to the mites.)

In the course of experiments to discover whether the mites could detect leaves of a food plant without actual contact, use was made of the Composite, *Tripteris clandestinum*, on which they readily feed in the field, and which is remarkable for the strong odour that the leaves give off when broken. A leaf was placed in one end of a glass tube. Some mites were put into the tube, which was then closed at each end with a plug of cotton-wool. It was found that the mites sought the more brightly illuminated part of the tube, quite irrespective of the position of the leaf. Then the leaf was removed, and a small rectangle was cut from it and put in the tube. This time the mites avoided the end of the tube which contained the cut leaf, even when this was pointed towards a source of light. The repulsion was even more marked when the rectangle of leaf was replaced by cotton-wool soaked in the juices of a crushed leaf. As was to be expected, no repulsion was found with cut pieces of sunflower (*Helianthus*) or clover (*Trifolium subterraneum*) leaves.

It appears from several tests that the mites are unable to detect a sugar solution until they come in contact with it. In fact, all the olfactory reactions discovered were negative, and no substance was found to attract the mites from a distance.

9. Special activities

(*a*) *Host-plant selection and feeding*

Providing physical conditions are uniform, the course followed by a mite running about on the soil is very erratic, owing to frequent changes of direction, often a more or less complete reversal; the result is a crossing and recrossing of a small patch of ground, rather than a migration from one place to another. The mite frequently pauses to apply its mouthparts to various surfaces. In

most cases it withdraws them almost immediately, or after a few seconds, and passes on in a new direction. Many of the changes of direction appear to be quite spontaneous, without any external stimulus; this is seen clearly when mites are put into a long glass tube, uniformly lighted.

When its wanderings bring it in contact with a plant, the mite frequently proceeds upwards, and runs about over stem, petioles and leaves, pausing at intervals to apply the mouthparts to the plant. If the plant is unsuitable as food the mite continues its wanderings until they lead it back to the ground. But when it arrives on a suitable part of a favoured food plant, such as a clover or a capeweed (*Cryptostemma calendulaceum*), its behaviour changes. After applying the mouthparts, it either remains stationary, or more often spends a number of seconds in turning this way and that, applying the mouthparts to different parts of the epidermis, as if seeking out a suitable spot at which to begin feeding.

Whether these apparent trial-and-error activities are at all governed by taste is uncertain. It may be that the stimulus is entirely a mechanical one, provided by the relative penetrability of different regions of the epidermis or other surface that is being tried. It is a well-known fact that the mites prefer to feed at broken edges of the leaf tissue such as those left by the clover springtail (*Smynthurus viridis* L.).

The position taken up on the plant is determined to some extent by lighting conditions: they tend to move from the gloomier parts to the more brightly lighted parts of the plant, e.g. to the apical parts in a dense growth of clover. On the other hand, they are repelled from the parts of the plants in bright sunlight. But in the spring, at times when the sunlight is not too intense nor too hot (e.g. towards sunset), the mites gather in large numbers on the *Cryptostemma* flowers, where they feed on the petals, on the succulent tissues of the florets, and apparently also on the pollen.

Swan gives a detailed account of the process of feeding, which consists essentially of a piercing of the cuticle and leaf cells by means of the mouthparts, and a drawing up of the cell contents as they well out.

(*b*) *Clustering*

A common phenomenon both in the field and in the laboratory is the crowding together of the mites into dense clusters. In the field, as noted by Tucker and Swan, this occurs chiefly in slight depressions in the soil, and less markedly on the leaves of food plants. The behaviour of the mites forming these clusters strongly suggests that the process is a response to tactile stimuli. They appear to be specially responsive to the touch of each others' bodies, and crowd together, often trying to stand one upon another. Often there are two or three vertical tiers of mites in parts of the clusters. Both nymphs and adults take part in their formation.

Although this clustering seems to be primarily a tactile response, it occurs only when physical conditions are favourable, i.e. when temperature is favourable, and atmospheric humidity high. In experiments (Solomon, 1937) in which temperature and humidity were stabilized, the mites were observed to crowd together at various temperatures from 10 to 30° C. provided the humidity was high. At high temperatures or in low humidity conditions the mites are restless and run incessantly, so that clustering cannot occur. At low temperatures they move about very little, so that there is little opportunity for clusters to form. The lowest humidity at which the crowding together persisted for a number of hours was 44% R.H. at 18° C. (sat. def. 9 mm.). However, it is difficult to set exact limits of humidity and temperature, because the phenomenon of clustering is itself vaguely delimited. Furthermore, it may continue for a few minutes only, or for hours or even days, according to the physical conditions. Mites that have been kept in a moist atmosphere may cluster together for a time even in dry air, providing temperature is favourable.

Allee (1931) has collected the available information about aggregations of this nature. They occur in animals of many groups, e.g. Enchytraeid worms, brittle stars (*Ophioderma*), land Isopods, aquatic Isopods (*Asellus*), certain caterpillars (*Hyponomeuta*, *Arye*), Gyrinid beetles and Silurid fishes (*Ameiurus*). The stimuli which lead to the formation of the aggregations are visual in some cases; in others (as in the first two examples mentioned above, and as appears to be the case in the earth mite) they are tactile. A comparison can be made between the clustering of *Halotydeus* and that of the terrestrial Isopods, for in both cases the aggregation is affected by temperature and moisture.

(*c*) *Web-spinning*

In the field mites have been observed occasionally spinning their fine white webbing on the leaves of clovers and capeweeds, on decaying vegetation, and even on the soil. In the laboratory they will spin on leaves, or on glass (as noted by Swan), and also on collodion film. Sometimes they bind down the body of a dead mite to the glass with a circular web.

A factor which influences the spinning of the web is the presence of moisture on the substratum. For example, mites will spin very readily on clover plants floating in a jar of water, so that their leaves are moist with fine dew, but usually not on similar plants growing openly in the laboratory. They also spin readily on a piece of collodion film floating on water. In the field, spinning occurs mostly in damp situations, but is sometimes observed on leaves that appear to be quite dry on the surface.

The process of web-spinning is easily recognizable. The mite, either gripping the substratum with its claws or (more often) running about over a small area, sweeps the hinder part of the body from side to side, rubbing the genital aperture (from the neighbourhood of which the silk is produced) over the surface of the substratum. The resulting patch of webbing consists of a network

of fine threads which cross and recross one another in a most irregular manner. A microscopic examination reveals small globules of water-like fluid spaced at intervals along the threads. Numerous spinning mites have been examined and some dissected. They are smaller than the fully grown egg-bearing females, and are very probably males.

(*d*) *Oviposition*

In the field oviposition occurs chiefly on the undersides of leaves that are resting on the soil, or close to it. Occasionally eggs are found higher up on the leaves or stems of plants. The leaves of the capeweed (*Cryptostemma calendulaceum*) are specially favoured. The eggs are distributed irregularly about the leaf surface, to which they adhere closely. These points were recorded by Tucker and Swan.

(1) *Texture.* Laboratory experiments indicate that the selection of surfaces for oviposition is governed chiefly by the texture of the surfaces. The first experiment bearing on this point was carried out by Tucker, who writes: "Leaves of spinach, pea and *Cryptostemma* were fed daily to captive colonies, and very rarely were eggs deposited on the pea leaves, though the mites fed well on them. Spinach leaves occasionally had a few eggs laid on them, but the majority were invariably deposited on the *Cryptostemma* leaves."

A group of mites was put on damp sand in a Petri dish with six leaves, three of soursob (*Oxalis cernua*) and three of clover (*Trifolium subterraneum*). The *Oxalis* is not eaten, while the clover is one of the chief food-plants of the mite. The leaves of the two plants are similar in shape and size, but very different in texture. After one day, the numbers of eggs on the three *Oxalis* leaves were 152, 245 and 50; on the clover leaves, 20, 1 and 0.

It was found that mites laid much fewer eggs on damp filter-paper than they did when supplied with capeweed leaves. When enclosed in a Petri dish with a capeweed leaf and a piece of damp filter-paper of similar size, a group of mites laid 37 eggs on the leaf, 3 on the paper.

When a piece of capeweed leaf and a similar piece of cellophane were supplied, mites in a Petri dish laid over 300 eggs on the leaf, none on the cellophane. Similarly, a group of mites laid over 200 eggs in 3 days on a capeweed leaf, and none on an adjacent leaf which had been coated with flexile collodion, in spite of the fact that the mites came to rest on it quite readily.

When mites were kept in moist conditions in a wide glass tube which was partly lined with damp filter paper, they laid (after 6 days) over 100 eggs on the glass, but none on the filter-paper. In other experiments, mites would not lay on paper, nor on gelatin.

(2) *Edibility.* It is indicated by some of the experiments in section (1) that suitability as food is not a factor influencing the choice of places for egg-laying. This was confirmed by the following experiment. Mites on damp sand in a Petri dish were supplied with a piece of capeweed leaf and two damp pieces of

filter-paper, one of which was moistened with sugar solution. Many mites were attracted to the sugar solution and fed upon it, yet in 2 days only 2 eggs were laid on this piece of filter-paper, while over 200 eggs were laid on the leaf. (No eggs were laid on the second piece of filter-paper.)

(3) *Position.* It has been remarked by all workers on the earth mite that it prefers the underside of a leaf for oviposition, particularly when this is close to the soil. As noted by Swan, if a leaf be turned over, the mites will then lay their eggs on what was formerly the upper side. Similarly, mites kept in a moist Petri dish will lay many eggs on the underside of the lid, relatively few or none at all on the vertical walls or the bottom. This seems to be the only well-marked response to gravity in the whole of the mites' behaviour.

Having found a suitable surface, the mites then select parts of it for oviposition. In this final selection they are guided to a considerable extent by stereotropism, i.e. they tend to select sites where their bodies can make contact with more than one surface at the same time.

A pad of folded moist filter-paper was put on damp sand with mites, in a Petri dish which was kept in the dark. One end of the pad was held up 2 mm. from the sand by a small strip of wood (Fig. 10). About 300 eggs were laid on the underside of the paper after 4 days, and most of these were grouped in an irregular belt across the middle, parallel to the strip of wood. In this region the backs of mites standing on the pad would probably be in contact with the sand. The remaining eggs were almost all distributed along the folds at the edges of the pad. In a repetition of this experiment the eggs were distributed chiefly along the angle between the paper and the supporting strip of wood, and also along the folds of the pad.

(4) *Moisture.* Although the mites will lay eggs on dry surfaces, they lay much more readily and abundantly when conditions are moist. It was found, for example, that mites would lay fairly readily on the sides of a moist glass vessel, but rarely on dry glass; and Swan's observation, that the mites would not lay on filter-paper unless it was kept moist, has been confirmed repeatedly. Experiments with local mites did not confirm Tucker's (1925) statement that "changes in food supply or atmospheric conditions likely to cause dying off of the mites results in increased egg-laying". For it was found that mites kept with green leaves under very dry conditions usually would not lay eggs, and field observations failed to reveal any increase in oviposition near the end of the season.

(5) *Light.* Swan remarks that "mites lay both by day and by night, but most eggs are laid in daytime". It will be noted that in the experiments in section (3) above, the mites laid numbers of eggs when kept in complete darkness. It seems, therefore, that light stimuli do not play any important part in oviposition.

(6) *Temperature.* Tucker states that oviposition increases as summer approaches, but the writer's observations are in agreement with those of Swan,

who found that oviposition decreased as the temperature rose. During the first 2 weeks of Sept. 1936, mites in the laboratory laid fairly freely (max. temp. about 22–26° C.), but by the end of the third week, oviposition had ceased (max. temp. up to 28° C.), although many of the mites were replete with apparently normal hard-shelled eggs.

Several batches of mites were kept under favourable moisture conditions in a cool incubator at 15° C., and supplied with capeweed leaves, but they continued over a week without laying and finally died with the eggs inside them. Further attempts were made, with similar results, up to 17 Oct. (It appears that the rising temperature has some permanent effect on the eggs, for eggs dissected from these mites and kept at 15° C. did not hatch, although a control series of eggs dissected from mites killed earlier in the season developed successfully under these conditions.)

Towards the end of the 1935 season a similar halt in oviposition was noted. The only explanation that can be offered is that exposure of the developing eggs to high temperature makes further development impossible, and that eggs are not laid unless development has reached a certain point.

(7) *Conclusion*. The foregoing sections (1)–(6) may be summarized by the statement that in the selection of oviposition sites, texture, moisture and position are important factors, taste (or edibility) and light are not important, while temperature has important indirect effects on the process of oviposition itself. But, even when the information in the foregoing sections is taken into account, oviposition is found to be unexpectedly erratic. For example, when mites are brought into the laboratory and placed in surroundings favourable for oviposition, they seldom begin laying at once, but usually require at least a day, and often 2 or more days, before beginning to lay. Once laying has begun, they may usually be moved from one container to another, and considerably disturbed, without any resulting stop in oviposition. Also, the number of eggs laid may vary considerably for the same group on successive days.

10. Discussion

When external and internal conditions are at the optimum, the earth mite is inactive, and groups of mites will form clusters. It seems that this quiescent state may be disturbed by internal changes, such as those leading to feeding or oviposition, or by changes in the external physical factors. The resulting activities may then be interpreted as efforts to overcome the disturbing agencies, either by relieving internal stresses or by escaping unfavourable external conditions.

(The term "optimum" is used here for convenience, although this implies a viewpoint that calls for justification. In another series of experiments (Solomon, 1937) it was found that the temperature and humidity conditions under which activity was reduced and "clustering" tended to occur were also the conditions under which the mites survived longest. Under other temperature

and humidity conditions, it was found to be roughly true that the greater the activity of the mites, the shorter was their survival period. For the purposes of this paper, the "optimum" conditions are those under which the mites will survive longest. Also, these conditions are the ones sought out by the mites; an exception is the case of mites exposed to low temperatures: they are inactive and survive for a long period, but very low temperatures are not sought out by the mites.)

The first sign that optimum conditions no longer obtain is that the mites begin to run. Running is their most usual activity, for optimum conditions are exceptional rather than usual, and most of the reactions to specific stimuli are simply modifications of this general activity of running. Associated with this activity is a set of "testing" activities—an exploring of the substratum by means of touch- and taste-organs.

These simple running-and-exploring activities are modified by reactions to special stimuli. The direction of running (besides being frequently changed apparently without any special external stimulus) may be changed in response to stimuli of light, heat and moisture (free water), and to tactile and olfactory stimuli. The speed of running is affected chiefly by the temperature, but also by the intensity of any stimulus to which the mite reacts.

The various stimuli to which the mite reacts seem to fall naturally into groups and subgroups, as below. This grouping is appropriate for the reactions as well as for the stimuli. With minor alterations, it could probably be applied to the behaviour of any animal having an action system of the same simple type as that of *Halotydeus*.

(A) *Internal stimuli*, e.g. hunger, the urge to oviposition. The immediate reaction is the running-and-testing activity, which brings the mite into relation with various external stimuli.

(B) *Indirect or diffuse stimuli*. These affect the general metabolism of the mite, and hence unavoidably affect its behaviour.

(1) *Temperature of environment*. This has an obvious effect on the speed of running, which tends to be greater the higher the temperature.

(2) *Atmospheric humidity*. This affects the evaporation of moisture from the mite, and the resulting effect on the metabolism is expressed in its behaviour: it tends to come to rest when the humidity is high, but in air of low humidity it soon becomes restless and runs continuously.

In both cases the effect of unfavourable conditions is to increase the running activity.

(C) *Direct external stimuli*. These operate directly through sense organs and nervous system, and any effects on the general metabolism are of secondary importance in so far as the reactions are concerned.

(1) *Continuous stimuli*.

(*a*) *Contact stimuli*.

(i) *Tactile stimuli*. The mites are repelled by the touch of certain substances (e.g. liquid paraffin) and attracted by the touch of others (e.g. certain leaves on

which they lay their eggs). In the latter case, the response is a reduction or cessation of the locomotor activities. Clustering and the stereotropic response provide examples of this.

(ii) *Gustatory stimuli.* In response to the taste of certain substances (e.g. sucrose solution), the mites cease their locomotor activities, and continue instead with the processes of ingestion.

(iii) *Moisture of substratum.* On a dry substratum the mites are restless and wander continually; on a moist surface, such as damp soil, their activity is greatly reduced, and (if temperature is favourable) clustering is likely to occur.

The reactions to these contact stimuli are of two types: negative reactions, resulting in resumption of running, and positive reactions, which cause the mites to stop running for some time, or at least to reduce their activity.

(*b*) *Distance stimuli* (contact with source of stimulus not necessary).

(i) *Direction of light from a source.* Except in bright sunlight, the mite is positively phototropic.

(ii) *Differential light intensity.* The mite tends to avoid very dim or very bright light.

(iii) *Differential temperature.* The mite avoids extremes of heat and cold.

(iv) *Volatile substances.* The mite is repelled by the vapour of various substances.

In all four cases, the direction of running at any moment is not necessarily determined by the direction of the stimulus, but the resultant direction of its movements taken as a whole is determined by the direction of the stimulus. In general, the stronger the stimulus, the less deviation from the direct response occurs.

(2) *Discontinuous stimuli.*

(*a*) *Change in light intensity.* A sudden and marked change results in a sudden increase of activity. The disturbing effect soon disappears and the mites return to their former condition.

(*b*) *Vibration.* Vibration of the substratum is best considered as a series of discontinuous stimuli. The response is the same as in the previous case—an increase in the speed of running, with more frequent changes of direction.

Very often in natural conditions an observed reaction is the result not of a single stimulus, but of two or more stimuli of different types. For example, on a hot day a mite moving in the shade of a plant, may be observed to turn back almost immediately on reaching the sunlight. In this case there are at least two stimuli concerned, the high light intensity and the unfavourable heat (both of the sun's rays and of the exposed sand). There may be also a third stimulus operating: the dryness of the exposed sand. Similarly, when mites retire to the shaded recesses under the plants, this may be due jointly to the favourable low temperature there, to the favourably high humidity, and perhaps to the absence of a strong hunger stimulus.

This fact does not detract from the value of an analysis which enables the mites' complex activities to be expressed in terms of simple reactions to each of the stimuli which together make up the pattern of their environment. The reactions of some of the higher animals to the pattern may be quite different from the reactions one would expect from a study of their responses to the separate stimuli. But the earth mite gives no indication of any such ability to react distinctively to "situations", nor would it be expected in a member of the Acarina.

(A possible exception to this statement is best illustrated by the experiment (Fig. 6) in which mites preferred the dim light under a board when free on the sand, but made for the brighter light when enclosed in a tube. This might be interpreted as an example of a special escape-reaction. But such an interpretation, besides running counter to the results of most of the other experiments on the light-reactions, is incongruous with the simplicity of all that is known of the rest of the mites' behaviour.)

There are certain significant similarities between the behaviour of the earth mite and that of the water mites (*Eylais*) studied by Agar (1925, 1927). The basis of the water mites' behaviour is a random locomotory activity in search of food (the crustacean, *Daphnia*), which is detected by touch. "If an *Eylais* is placed in a large vessel of water it displays a ceaseless activity, swimming rapidly round and round, up and down, and turning sharply hither and thither" (Agar, 1925). They avoid high temperatures, but, as in the earth mite, the reaction is not a direct one: it is brought about as a result of frequent changes of direction, the turnings being more frequent the more unfavourable the conditions. This simple action system, based on the principle of trial-and-error, seems to be correlated with the simple mode of life of the water mites (Agar, 1927).

The earth mite, being a terrestrial animal, leads a somewhat more complex existence than the water mites. It is equipped with telereceptors and has a more extensive range of activities and a greater variety of micro-environments to choose from. But the basis of its action system is essentially the same—a ceaseless activity in response to external unfavourable conditions or to internal physiological requirements.

11. Summary

1. The reactions to the physical and chemical stimuli to which the phytophagous mite (*Halotydeus destructor*) is exposed were observed and tested experimentally; also the effect of these stimuli on the special activities such as host-plant selection and oviposition.

2. The mite is positively phototropic, except when in very bright light, such as strong sunlight; if no bright source of light is visible, the mite selects a subdued light, avoiding bright light and darkness.

3. It avoids extremes of temperature, but between these limits its selective activity is not marked: the higher the temperature, the greater is the mite's activity.

4. It has no strongly developed selective behaviour in relation to atmospheric humidity; but is more active, the lower the humidity; it selects a moist soil; free water is usually avoided.

5. There is no geotropic reaction, except that for oviposition the underside of a horizontal surface is preferred. The palps and forelegs serve as tactile organs; the mite is attracted by the feel of some surfaces, repelled by that of others; it is stereotropic under favourable physical conditions; it is made restless by vibration; there is no anemotropic reaction.

6. It is attracted by the taste of some sweet substances but is indifferent to others. It is repelled by the vapours of many volatile substances.

7. Host-plant selection is the result of random wandering with repeated trial-and-error testing of the substratum by means of tactile and gustatory organs.

8. The crowding together of the mites into dense clusters seems to be a tactile reaction, but occurs only when physical conditions are favourable.

9. Web-spinning is probably a male characteristic and depends to some extent on the presence of moisture.

10. In the selection of oviposition-sites (the undersides of *Cryptostemma* leaves are preferred), texture, moisture and position are important factors, taste and light are not important, while a high temperature (about 28° C.) puts a stop to all further oviposition.

11. In general, the activity of the mites under certain favourable conditions is subdued, and they usually crowd together. But conditions (internal and external) at most times depart to some extent from the optimum range; this calls forth the more vigorous activity of running, with occasional turns, and frequent testing of the substratum by means of tactile and gustatory organs. This is the basis of the action system, for reactions to special stimuli consist of modifications of the simple activity of running. The running is modified in response to the indirect or diffuse external stimuli of temperature and atmospheric humidity, to the contact stimuli of texture, taste and moistness of substratum, and also in response to the distance stimuli of light, heat and vapours of volatile substances. Also, the mites are disturbed to more vigorous activity by the discontinuous stimuli of sudden light-change and vibration.

Acknowledgements

This work was done at the University of Western Australia during the tenure of a Hackett Research Studentship for which I wish to make grateful acknowledgement. I am indebted to Prof. G. E. Nicholls and to Prof. J. E. Nichols, in whose departments of Biology and Agriculture respectively the research was carried out. For critical readings of the manuscript I am indebted

to Prof. W. E. Agar of the University of Melbourne, to Prof. J. E. Nichols, and to Dr A. J. Nicholson, Chief of the Division of Economic Entomology, C.S.I.R., Canberra. Also I have had the benefit of helpful discussions with my colleague, Mr K. R. Norris.

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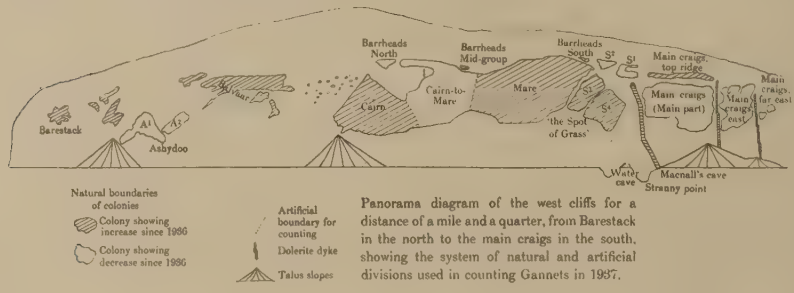
THE 1937 CENSUS OF GANNETS ON AILSA CRAIG; WITH NOTES ON THEIR DIURNAL ACTIVITY

By H. G. VEVERS, JAMES FISHER, C. H. HARTLEY and ALAN T. BEST

(*With 2 Figures in the Text*)

1. The census

In 1936 (**1**) a census of gannets (*Sula bassana*) was undertaken on Ailsa Craig by Vevers & Fisher, in which a direct count was made and a method of estimation described, by correlating the alighting activities of the birds. Though this method has since been described as "exceedingly difficult to carry out", yet we claim that it is possibly the most rapid and accurate method of estimating populations on cliffs where the distribution is irregular. It must be further explained that the 1936 census was carried out entirely by means of direct counts, while the alighting method was only used experimentally.



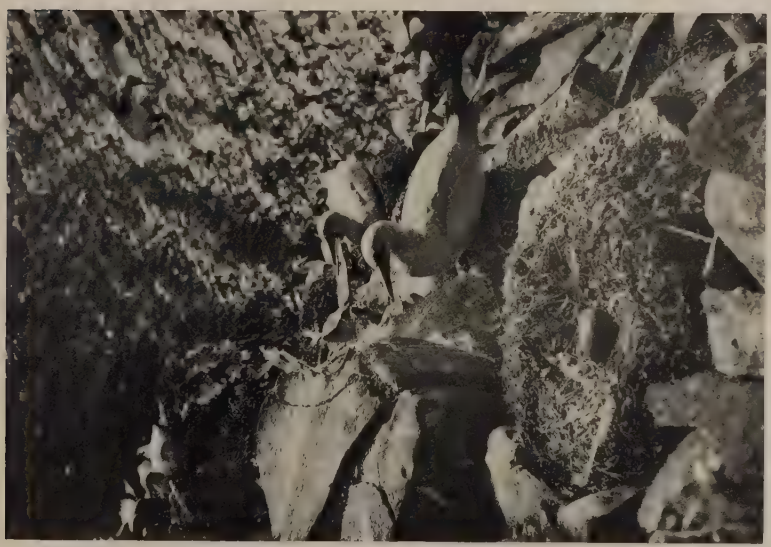
Panorama diagram of the west cliffs for a distance of a mile and a quarter, from Barestack in the north to the main craigs in the south, showing the system of natural and artificial divisions used in counting Gannets in 1937.

Fig. 1.

This year's census was done by a combination of direct counts and the use of the alighting method. As explained in the previous paper the use of direct counts was possible at the time of year at which the work was done, but owing to the size of the gannet colony on Ailsa Craig, and the fact that the largest aggregations, such as the Mare, are not easily subdivided, it was found quicker in such cases to use the alighting method. The census itself occupied the days 6–13 April, whereas in the previous year it was carried out from 7–16 April.

For a control in the use of the alighting method we took the Main Craigs (Main part), since this was the cliff we had used experimentally in 1936; it was also the group we had under continuous observation for the purpose of examining the diurnal activity of the gannets. The mean of two counts of the total number of nests on this was 346·5 (340 and 353). Our complete results are shown in the following table; in the case of S 3 and S 4, where we had a direct

Phot. 2. Oiled gannet.



Phot. 1. Nesting gannets.

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count as well as an alighting estimation, we have used the result of the direct count for the total. Some of the grouping had changed since last year; for instance, on the Barestack the numbers and the size of the groups had altered and we no longer kept the lettering B 1–B 6, but counted the group as a whole. On the Barrheads the distribution had also changed and we estimated part of the north group in our alighting census of the cliff between the Cairn and the Mare.

Cliff		1937 direct count: Counts	1937 direct count: Mean	Alighting method (1937)	Increase + Decrease −
Barestack		147	147	—	+
Northwards of Ashydoo		370	370	—	+
Ashydoo	A 1	186, 188, 190	188	—	−
	A 2	34	34	—	−
Balvaar		646, 653	649·5	—	+
Balvaar-Cairn		67, 68, 69	68	—	+
Cairn		—	—	813·7	+
Barrheads	S.	43	43	—	+
	Mid.	14	14	—	+
	N.	90 & 93	91·5	—	
Cairn-Mare and part of N. Barrheads				290	−
Mare		—	—	1936	+
Mare-Stranny Point	S 1	85, 87	86	—	−
	S 2	61, 62, 62	61·7	—	−
	S 3	170, 172, 176, 178, 180	175·2	(427·1)	+
	S 4	260, 272, 275	269		+
Main Craigs	Top	263, 270	266·5	—	+
	Main part	340, 353	346·5	—	−
	East	75	75	—	−
	Far East	20	20	—	−
	Totals		2904·9	3039·7	
	Grand total (1937)		5944·6		+

Total in 1936, mean of two counts by different observers: 4799.

The areas showing an increase are shaded in Fig. 1, while those showing a decrease are left unshaded. It is noticeable that the general increase of 23·9% has taken place (*a*) in the thickly populated colonies, and (*b*) particularly on the tops of the cliffs. Without wishing to draw any sweeping conclusions, we think there is no doubt that this must throw light on the plasticity of the choice of nest

site in the gannet, and that we must be particularly careful before making any generalizations on the amount of territorial behaviour in gannets and on the amount of space any individual pair needs in the colony. The East and especially the far East parts of the Main Craigs are of interest, as colonies on them had increased after the quarrying on the southern coast lapsed in 1925 6, but are now starting to decrease.

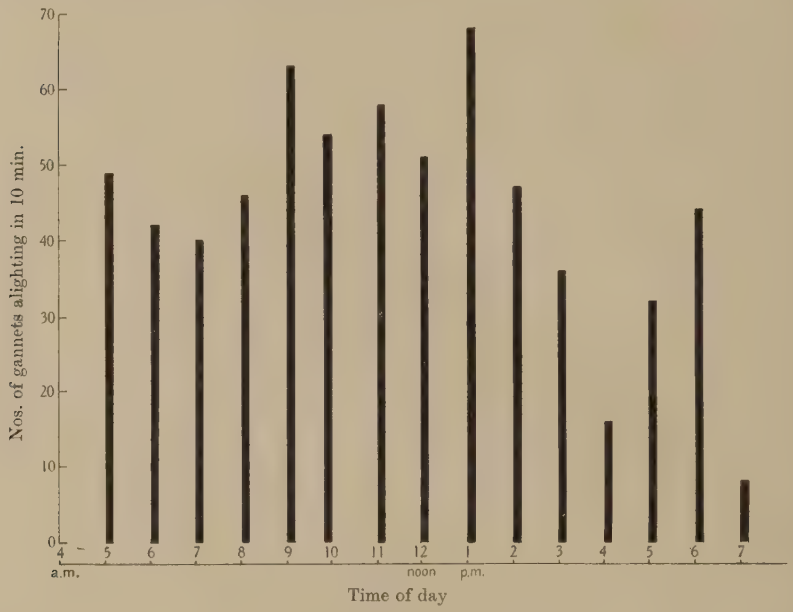

Fig. 2. Hourly readings on 12 April 1937.

Finally it is necessary to mention the effect on the population of mortality by oiling. It is well known that the oil which finds its way from ships on to the surface of the sea, either by mistake or carelessness, is often found covering the feathers of a large number of sea-birds, in particular guillemots, razorbills, and puffins. It is not generally realized, probably owing to the inaccessible nature of their colonies, that gannets are also susceptible to the effects of oiling. During April a large number of oiled gannets, together with various "auks", were dying on the shore at Ailsa Craig, being unable to fly, dive, or feed. On 10 April there were 22 oiled gannets on the coastline of 2·5 miles, the total number of oiled birds of all kinds being 83. The effect of this kind of mortality occurring sometimes two or three times a week during the spring months must be considerable, although it probably does not approach the number killed throughout the year by breaking wings during storms.

2. Diurnal activity

On the suggestion of Prof. James Ritchie we attempted to use the alighting method for investigating the diurnal activity of the gannets, taking as a sample our control group of the Main Craigs (Main part).

Ten-minute counts were made daily at 6.00, 12.00, and 18.00; at the same time we swung wet and dry bulbs, and noted wind and general weather conditions. The last observations were empirical, as we had no anemometer or photometer. From graphic plots of the temperature and relative humidity we have found no significant correlation. The failure to produce a correlation is comparable with the failure of two of the authors to link kittiwake activity with weather conditions in Spitsbergen (**2**). A plotting of wind observations, however, seems to indicate some relation between activity and wind.

On 12 April we made counts at hourly intervals from dawn till dusk. A graph of this (Fig. 2) shows that there is possibly a distinct diurnal rhythm. There were no signs of activity among the gannets until just before 5.00, that is while it was still dusky, although the guillemots and razorbills were already flying. The amount of activity seemed to fall off between 5.00 and 8.00, and then to increase noticeably between 9.00 and 14.00. Owing to the restricted nature of these observations, further conclusions are not justified at this stage.

3. Summary

1. A further census of gannets (*Sula bassana*) on Ailsa Craig, by a combination of direct counts and the alighting method, gave approximately 5945 nests, an increase of about 24% on the previous year's census.

2. This increase was found to be localized in definite regions.

3. The effect of oiling on the population of gannets is considered.

4. The use of the alighting method in correlating the diurnal activity of the gannets, suggested a relation between activity and wind, and the possibility of a distinct rhythm.

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THE CALCULATION OF SOIL POPULATION FIGURES

By K. D. BAWEJA

Rothamsted Experimental Station, Harpenden

(*With* 1 *Figure in the Text*)

In the investigation of the soil fauna, it is customary to express population figures in millions per acre. They are calculated with respect to surface area and to a depth sufficient to include the major portion of soil population. Usually a depth of 9 in. has so far been preferred. From the observations carried out at Rothamsted Experimental Station in 1936 it was seen that

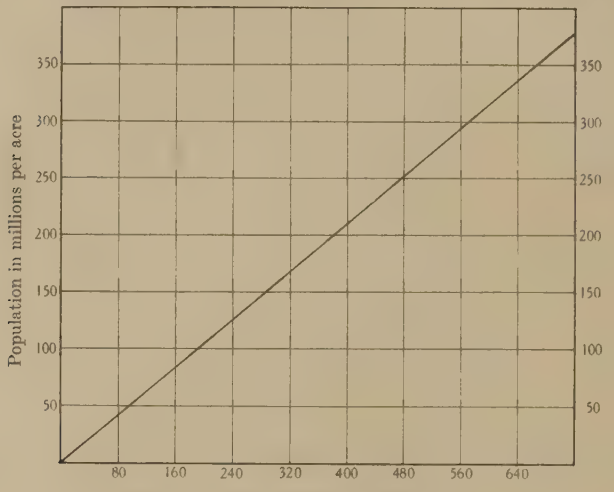

Fig. 1.

80-90% of the soil fauna was restricted to the top 9 in. Since it is a convenient depth that meets practically all the requirements, particularly with respect to faunal and agricultural conditions, it had so far been adopted in this country.

Owing to the surface area of the samples taken being in sq. in., frequently some time has to be spent before an approximate figure of millions per acre can be obtained. It would be an advantage if such figures, particularly in field observations or during discussion on soil fauna density, could be rapidly worked out. In other words, the size of the sample should be so selected that it allows

of a rapid calculation from numbers per sample to millions per acre. Unfortunately all the sizes previously employed offered no such facility.

The size of the sample 3×4 in. employed during some recent investigations at Rothamsted overcame to a great extent this difficulty of calculation. This small plot is exactly 2/1,044,440 of an acre, so that if the number of the individuals per sample be divided by 2, a figure is obtained of the population in millions per acre which is correct within 4·5% (under-estimated). For all populations up to 20 individuals per sample the figure of $X/2$ is correct to the nearest million. Above it to a figure of 700, which is an unusually high concentration for the sample, a correction can be made by adding 1 million for each 40 individuals, i.e. about 5%. This corrected figure gives slight under-estimation for population figures up to about 220 individuals per sample and very slight over-estimation above this value (Fig. 1).

Numerically it may be expressed as follows:

$$\frac{X}{2} + \frac{(X-20)}{40},$$

where X represents the number of soil organisms per sample. To illustrate the above expression suppose the number of soil organisms in the sample is 460, the soil population figures will work out as follows:

Approximate population

$$\frac{460}{2} + \frac{460-20}{40} = 241{\cdot}0 \text{ millions per acre.}$$

The exact population in this case is 240·4 millions per acre. The difference between the two is very slight and can be safely ignored.

CANADIAN ARCTIC WILD LIFE ENQUIRY, 1935–36[1]

By DENNIS CHITTY and CHARLES ELTON
Bureau of Animal Population, Oxford University

(*With 4 Figures in the Text*)

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1. Introduction

Periodic fluctuations in the catch of arctic foxes (*Alopex lagopus*) in the Canadian Arctic were discussed by Hewitt (1921), who published a diagram showing the white fox fur returns of the Hudson's Bay Company from 1850 to 1914. He pointed out that this curve showed a marked short-period cycle which averaged about four years in length.

This fluctuation, which causes alternate periods of plenty and dearth, has been commented on by many travellers in the North, and has been for many years a vital factor in the Arctic fur trade, and therefore in the whole economy of white men and natives alike.

The archives of the Hudson's Bay Company contain a large body of facts which confirms the existence of this four-year cycle in fur, and proves that it is due to a real fluctuation in numbers of the fox population, often over huge tracts of country in the same year. A full analysis of this material is being published elsewhere (Elton MS.).

A similar cycle in fox populations has been noticed in other parts of the world, notably in Norway, where it is associated with regular fluctuations in the voles, mice and lemmings upon which the foxes feed (Elton, 1924, 1925; Johnsen, 1929).

The analogy with Norway, and a good many scattered observations reported from the Canadian Arctic, make it probable that there is also in the populations of Canadian Arctic lemmings (*Lemmus* and *Dicrostonyx*) a cycle which may control the numbers of foxes.

[1] Promoted by the Northwest Territories Administration of the Canadian Government, Ottawa.

The arctic fox is subject to epidemic disease which usually breaks out at the end of the peak abundance. At this time there is often an unusually great southern migration of foxes. The disease in its symptoms resembles closely one of the important pandemic diseases (probably a form of encephalitis) which breaks out at intervals among dog teams in the Arctic, causing very severe mortality and consequent shortage of dogs, loss of mobility and hardship among the people.

A preliminary enquiry, through the Hudson's Bay Company, into the distribution and occurrence of the fox and dog epidemics (Elton, 1931) suggested an identity of the two diseases and some correlation in the outbreaks.

Another feature of the Arctic cycle is the periodic multiplication of snowy owls (*Nyctea nyctea*) which live mainly on lemmings. Gross (1927, 1931, 1935) has found that these white owls flock down in large numbers into the eastern United States every four years or so, and that this irruption coincides with the arctic fox cycle and is presumably caused by scarcity of lemmings in the Arctic.

A brief general description of the Arctic cycle has already been published (Elton, 1934). Its wide extent and surprising ramifications led the Lands, Parks and Forests Branch, of the Department of Mines and Resources, Ottawa, to initiate an annual questionnaire enquiry at a number of Arctic stations. The Bureau of Animal Population was asked to take charge of the framing of the enquiry and mapping of the results, since it already carries out the Canadian Snowshoe Rabbit Enquiry along similar lines for the Canadian National Parks Bureau, and also because it has a very large amount of information derived from the Hudson's Bay Company and other sources. The Hudson's Bay Company had been supplying annual reports on wild life since 1925, and it was arranged that the 1935-36 reports should be included in the present enquiry. Copies of the questionnaire replies and of the Hudson's Bay Company reports concerned are deposited with the Northwest Territories Administration, Ottawa, which now handles the affairs of this area, and in the Bureau of Animal Population.

We wish to acknowledge the full co-operation extended by the authorities in Ottawa through Dr Charles Camsell, Commissioner of the Northwest Territories, and Mr R. A. Gibson, Deputy Commissioner of the Northwest Territories; also to thank the numerous observers whose replies have made the enquiry possible. We are also indebted to the Governor and Committee of the Hudson's Bay Company for permission to use their reports, and to Mr Ralph Parsons, Fur Trade Commissioner of the Company in Winnipeg, for his active interest and help.

The enquiry is being made for a second year (1936–37). It is hoped that it may be kept going for some years in order that the features of periodicity may be mapped and analysed, for comparison with climatic and other fluctuations. The continuity of the work at Oxford has been secured for several years by

a grant to the Bureau, for expenses, from the Carnegie Corporation of New York, administered through the Carnegie Institution of Washington, to whom grateful acknowledgement is made.

2. Questionnaire

The enquiry covered five animals: arctic fox, lemming, snowy owl, ptarmigan, sledge dog. The ptarmigan was included because it is subject to fluctuations that are not well understood. The report on it is being deferred until more information has accumulated.

The following form of questionnaire was used for the arctic fox, lemming, snowy owl and ptarmigan:

1. To what region do your observations refer? (Please describe the district in such a way that it can be identified on the map.)
2. Were arctic fox *more abundant* or *less abundant* than in the previous twelve months?
3. Were they unusually abundant or unusually scarce?
4. Have they been subject to epidemic? If so, in what months?
5. Have they been migrating? If so, in what months?
6. Remarks.

Name:

P.O. address:

Note: Please make necessary observations and submit your replies on or about the 31st May, 1936.

For the sledge-dog questions 2–5 were different:

2. Have sledge dogs in your district been subject to epidemic or disease?
3. What were the symptoms of the disease?
4. In what month of the year did it occur?
5. To what cause do you attribute the disease?

The Government enquiry produced 120 replies. These include a certain number from Hudson's Bay Company posts. The others are from members of the Royal Canadian Mounted Police, fur-traders, etc. The Company's posts also returned reports directly to the Bureau, these being on a slightly different plan. Some extra information from these has been included, which brings the total number of observers up to 163. The period covered by the replies includes the winter trapping season and the previous summer breeding season.

3. Methods

Two features of the enquiry require explanation: (*a*) the identification of species and their distribution, (*b*) the method of noting comparative abundance and the methods of mapping the records of population change.

(*a*) *Species*

(1) Arctic fox (*Alopex lagopus*). There is no question of incorrect identification with this species, which is easily recognized, and widely known through the fur trade. It is called "white fox" in the Canadian Arctic, where the

dimorphic "blue" phase is rare. The white fox is brown in summer, but much smaller than its relation the red fox (*Vulpes fulva*) whose range overlaps.

The main principle we have followed is to map reports from the breeding area of each species. In certain years the fox migrates far south of its breeding area, which is normally the high Arctic and barren lands north of the tree-limit. These southern movements are generally assumed to be caused by food scarcity in the North. As it is important to obtain information about them, we have, for the Eastern Arctic, not only mapped the records from about the tree-limit northwards, but also those from the whole coasts and parts of the hinterland of Hudson Bay and James Bay and the coast of Northern Labrador. Much useful information about migration is contained in the reports, but has been reserved for future study.

Evidence from many earlier Hudson's Bay Company reports and fur returns shows that arctic foxes frequently have a southward "run" down these coasts. Part of this migration is believed by fur traders to be due to movements of the sea-ice, on to which many arctic foxes go in the winter time.

In the Western Arctic we have used certain arbitrary boundaries: the tree-limit (which is not as abrupt in reality as it appears on maps); Great Slave Lake east of Fort Rae (on the northern arm) and east of Fort Resolution (on the south shore); Great Bear Lake; and the Delta of the Mackenzie River. We have omitted most of the Mackenzie River Valley, where arctic foxes are seldom seen. In this connection the following reports are relevant:

Report No. 50 (Group 10), states that "the arctic fox is not caught in the defines of this district, and very few are ever seen; it belongs to the more northerly districts and to the barren lands of the east end of Great Slave Lake". No. 55, covering the districts round Fort Providence and Hay River Settlement, states that the arctic fox is unknown there. No. 51, covering a 30 mile radius from Cameron Bay Settlement, west shore of Great Bear Lake, states "there are very few arctic fox in this district". No. 65, from the same area, notes that "arctic foxes, except for an occasional stray, are not reported from this section, but are found North and East from this point". Several observers (Nos. 57, 108, 109, 111, 113, 114, 115) in the Arctic Red River and Thunder River areas on the lower Mackenzie River, agree in reporting rarity of arctic foxes. No. 57 (Point Separation) states "There are no arctic fox in my district. I have only killed two in ten years." In the Arctic Red River area only one or two have been caught in the last five years.

(2) Lemming (*Lemmus* and *Dicrostonyx*). In the following description we are indebted to Dr R. M. Anderson of the National Museum of Canada for comments and corrections. His reports (1934, 1937) on the mammals of the Canadian Arctic may be referred to for further information. Lemmings are the commonest small rodents of Arctic regions, and the only mouse-like rodents found at all on the larger Canadian Arctic islands. *Lemmus* has a rather striking pattern of rich colours, and does not turn white in winter. It is absent from the Quebec Peninsula. The Back lemming (*L. trimucronatus trimucronatus*) occurs widely in the high Arctic and barren grounds from the eastern edge of the Mackenzie River delta across to Hudson Bay. It ranges south to Artillery Lake and Thelon River, and is also found on Baffin Island (including Bylot Island), Southampton Island, and the southern portions of

Banks and Victoria Islands. Another subspecies, the Alaska brown lemming (*L. trimucronatus alascensis*) inhabits the Arctic west of the Mackenzie delta. *Dicrostonyx* has more sober colours in this part of its range, being generally greyish or brownish with a dark dorsal stripe. It turns white in winter, when it also grows long cleft claws. *D. hudsonius* occurs on the barren lands of Quebec Peninsula, ranging up to the Arctic coast. Its southern limit on the Northern Labrador coast is Hamilton Inlet. Several forms inhabit the Western Arctic and northern islands. With the increase of material available for taxonomic study there have recently been some changes in the names, for a discussion of which see Degerbøl (1935). The Richardson collared lemming (*D. groenlandicus richardsoni*) ranges from the north-west shores of Hudson Bay (its southern limit being at Fort Churchill, i.e. about the tree-limit) across the barren grounds and Arctic coast to Great Slave Lake and Bathurst Inlet. At about Coronation Gulf this form grades into another (*D. groenlandicus rubricatus*) –the Alaska collared lemming, which is much more brilliantly coloured, and ranges west to Alaska. It also occurs on the southern parts of Banks and Victoria Islands. On the other large northern islands, including Baffin Island, the grey *D. groenlandicus* occurs. According to earlier naming (see Hinton, 1926), the two subspecies *richardsoni* and *rubricatus* belonged to a species *rubricatus* which is now abandoned. There is in all three subspecies intergrading in certain regions.

In most parts of the Canadian Arctic north of the tree-limit, there are therefore two kinds of lemmings, the species varying. In Quebec Peninsula there is only one. Besides these, there are several species of voles or meadow mice which range far northwards, but are not known to come on the big islands. These include *Microtus aphorodemus* on the west coast of Hudson Bay (known, for instance, from Eskimo Point); and *M. pennsylvanicus labradorius* and *M. enixus* in Quebec Peninsula, both ranging to Ungava Bay.

Dr Anderson provides the following note on the north-western species: "The Drummond meadow mouse (*Microtus pennsylvanicus drummondi*) ranges north from the Prairie Provinces to the limit of trees, if not beyond, in Mackenzie delta, lower Anderson River and lower Horton River within twenty miles of Franklin Bay. The MacFarlane tundra mouse (*Microtus operarius macfarlani*) is found in east central Alaska and central Yukon, and ranges along the Arctic coast from Mackenzie delta to Franklin Bay. The writer found it very abundant at Langton Bay in 1910 and 1911, but less common in spring 1912 (see Anderson, 1937, pp. 112–13)."

The reports about lemmings have been mapped for the region near and north of the tree-limit. In certain instances, where reports (mostly from Hudson's Bay Company posts) have mentioned increase or abundance of "mice" as well, this information has been included in Table 1, though not on the map. A few of the "lemming" reports may have referred to voles; but it is not thought that this error is important, as lemmings are being studied

in this enquiry primarily as an index of the rodent food available for predators.

(3) Snowy owl (*Nyctea nyctea*). Mapping was mainly confined to the breeding range, which is northwards from about the tree-limit, including the barren grounds. In winter this species migrates southwards, and in certain years it appears in large numbers, in the early winter, as far south as New England, as in 1926–27, 1930–31 and 1934–35 (Gross, 1927, 1931, 1935). It was not thought practicable to attempt complete mapping of these southern movements in the present enquiry; but we have included the same southern areas as in the fox map. Such mapping would also be liable to certain errors in identification. Although the snowy owl is the only large white owl in the Arctic proper, there is a very pale phase of the great horned owl (*Bubo virginianus*) with which confusion is possible. Taverner (1928) says: "The extreme of whiteness is shown by the arctic horned owl (*Bubo virginianus subarcticus*) that in certain cases may be almost pure white, with little ochre showing anywhere, and the black pattern very much reduced in prominence. It inhabits the Northwest Territories, the northern parts of the Prairie Provinces, and probably parts of the Yukon." It is, however, a forest bird, and is to be distinguished by its "horns", as well as details in plumage. This possibility of confusion led us to omit "snowy owl" records from the Mackenzie River Valley south of the Delta.

We are indebted to Dr P. A. Taverner of the National Museum of Canada, Ottawa, for information upon the distribution of the snowy owl and upon the extent to which there is likely to have been confusion with other species of raptors. The white gyrfalcon (*Falco islandus*) mentioned by some observers is stated by Dr Taverner in a letter of 6 July 1937 to be "ordinarily too scarce to introduce a very serious error".

(*b*) *Mapping*

In the present paper a beginning has been made in the use of both area and number of observers for estimating relative abundance of animals from questionnaire replies. The two methods make use of slightly different approximations to the truth, but in this instance have given practically the same results.

The primary data are those summarized in heavy type in Table 2, namely the *actual number* of observers in each category of relative abundance. The secondary data (smaller type, Table 2, and Figs. 1, 3 and 4) have as their basis the *area covered* by the observers. The workings of this system are briefly as follows. For each animal the areas are marked in on tracing paper over detailed maps. On a blank map these areas are then filled in with arrows, of which the direction indicates the nature of the observation, and the number the approximate square mileage involved. Since the length of each arrow corresponds to a distance of 50 miles, an arrangement end to end in paralle

Fig. 1. State of the arctic fox population in 1935–36 compared with 1934–35. Arrows indicate the areas covered by observers reporting INCREASE (↑), DECREASE (↓), and NO CHANGE, NOT ABUNDANT (←). Black dots are Hudson's Bay Company posts, etc. (1927 map). Broken lines show main vegetation zones.

Fig. 2. Prevalence of disease among sledge dogs in 1935–36. Reports of disease are indicated – ; disease absent or in minor proportions o. Black dots are Hudson's Bay Company posts, etc. (1927 map). Broken lines show main vegetation zones.

Fig. 3

Fig. 4

Figs. 3 and 4. State of the lemming and snowy owl populations in 1935–36 compared with 1934–35. Arrows indicate areas covered by observers reporting INCREASE (↑), DECREASE (↓), NO CHANGE, ABUNDANT (→) and NO CHANGE, NOT ABUNDANT (←). Black dots are Hudson's Bay Company posts, etc. (1927 map). Broken lines show main vegetation zones.

rows at "50 mile" intervals will represent an area in square miles of 2500 × the number of arrows.

In making the present maps, however, the aim has been to present a comprehensive visual picture of events rather than statistics reckoned on a basis of area. This year's procedure may undergo modification as a result of experience and criticism, and it should be realized that for the time being the main value of the maps is diagrammatic.

Where two local observations are made at less than 50, but more than 25 miles apart, the two are shown by separate arrows. For the most part, however, arrows are arranged in a pattern determined by the total area covered rather than by the number of observers (for which the tables should be consulted). Two arrows in disagreement within the same area are put closely side by side or crossing each other. For coastal strips, small islands and purely local observations, the arrows exaggerate the square mileage, while for inland observations they probably represent less than the actual area reported on. The area covered by observations on the arctic fox, for example, as a very rough estimate, is somewhere about half a million square miles.

Observations have been divided into ten or eleven groups and the data are presented regionally. Where an observer reports on an area overlapping more than one of these regional groups he is given a whole vote in one group only (Nos. 31 and 33). Where an estimate of relative abundance differs for two areas within the same group a half vote is given for each (No. 4). In Table 1 opinions of actual abundance (generally less reliable for statistical purposes than comparative estimates) have been reduced to the following categories: "rare" (r.), indicating that the animal seldom occurs at any time; "very scarce" (v.s.), including "none seen this year"; "scarce" (s.); "abundant" (a.) and "very abundant" (v.a.). ("Very" also includes "unusually", "exceptionally", etc.) There then remains a type of remark (rendered by × in the table), which generally indicates that conditions of abundance were not such as to attract particular attention. This is expressed by answers to question 3, such as the following: "normal", "average", "usual numbers", "fair", "no", "neither unusually scarce nor unusually abundant".

For the sledge dog a circle on the map indicates one or more reports that disease was entirely absent; or present, but not serious. A plus indicates reports of disease, usually in epidemic proportions. One circle or one plus only is placed either about the centre of each area or at the headquarters of the observer.

The arrows and plus signs are printed in rows on gummed paper and cut out. When stuck on the map their white borders sometimes cover up parts of the map and these are later inked in over a light-screen.

The map used this year is inaccurate in several respects, particularly in the position of the tree-limit. An improved blank map is in course of preparation for use in future years.

4. RESULTS

Arctic fox. It is obvious from the map and from Table 2 that compared with 1934–35 foxes had declined in numbers over almost the whole of the region covered in this report. 91% of observers reported decrease (arrows pointing down on the map) and not one estimate of numbers was received that fell into the classes "abundant" or "very abundant". In a few places foxes were stated to have been less abundant than for many years. There was only one mention of disease. No. 68 (Group 10) states: "White foxes were plentiful in this district (Ptarmigan L., Clinton Colden L.) in the winter 1933–34. This winter most of those caught were in very poor condition, some mere skeletons. Young were late in maturing. Looks as if disease of some sort attacked them last spring or summer."

Lemming. There was at least one report of lemming increase in each of the ten groups of observations. Altogether 37% of observers claimed an increase (arrows pointing up) and in a few places the animals were stated to be abundant. In most places, however, the increase was very slight, e.g. No. 79 (Group 7): "During the past year not more than a dozen lemming tracks have been noticed. During the previous year no tracks were noticed." Over half the observations indicate a decrease.

Snowy owl. 57% of observers reported decrease; 18% no change, not abundant (arrows horizontal, pointing left) and 25% increase. It is interesting that many of the latter reports come from places where lemmings or mice are also reported on the increase or abundant (for mice see Table 1). This correlation is especially noticeable on the west coast of Hudson Bay (Group 4), Southampton Island (Group 5), south-east Baffin Island (Group 6), and in the Fort Rae area (Group 10) where abundance of snowy owls and of mice is reported.

If this correlation should be established as a regular feature of the cycle, then increase of the snowy owl might be a good indication of higher fox populations in the season following. For it is likely that the snowy owl, being the more mobile of these two predators, would precede the arctic fox to those areas where the food supply was improving.

Sledge dogs. Epidemic disease among sledge dogs in the Canadian Arctic has often taken the form known there as "crazy disease", the symptoms of which resemble encephalitis. The animals run about in a strange manner, foam at the mouth, become very weak and often paralysed in the hind legs, and die. Mortality in dog-teams is very severe. These symptoms vary greatly, and overlap with those caused by distemper and other diseases, and it is unsafe to draw definite conclusions about causes from the symptoms alone. But broadly speaking the "crazy disease" seems to be the chief epidemic disease among dogs in the Arctic.

In Table 3 (*a*) and (*b*) are given all reports of the presence of disease. In

Table 3 (*c*) and in the last column of Table 1 are given all definite reports of absence of disease. In the Hudson's Bay Company questionnaire a space is left for observations on disease in sledge dogs so that absence of remarks is a fairly safe indication of absence of disease. However, use has not been made of this assumption in constructing the map.

Disease is reported as almost entirely absent from the Eastern Arctic during 1935 36. On King William Island and several other Western Arctic localities, however, there seem to have been outbreaks of disease, mainly of "distemper", as in the vicinity of great Slave Lake. The "crazy disease" does not seem to have been prevalent and in most places the teams are reported quite free from serious disease.

Table 1. *Summary of original data on arctic fox, lemming, snowy owl and sledge dog (part) for* 1935–6

The following abbreviations are used: I. = increase, D. = decrease, N. = no change, r. = rare, s. = scarce, × = not noticeably scarce or abundant, a. = abundant, v. = very. M. (preceding one of above) indicates reference to mice. An asterisk * marks those instances where observations on a particular animal were made in an area slightly different from the description in the table.

Sledge dogs: 0 indicates a report that disease was entirely absent. 0^{2-5} = report of disease in minor proportions as specified in Table 3 (*b*). $+^{1,\,6-13}$ = prevalent disease as specified in Table 3 (*a*). Bracketed observations in the sledge dog column are represented by the same symbol in the map.

Numbers in heavy type are the serial numbers of the replies to the government questionnaire. Unnumbered replies were received directly from the Hudson's Bay Company.

	Fox	Lemming	Owl	Sledge dog
Group 1. Northern Labrador coast				
Frenchman's Island, nearby islands and 20 miles inland	D. s.	—	D. s.	—
Cartwright	D. v.s.	—	D. v.s.	—
Rigolet half-way south to Cartwright; north half-way to Makkovik; west one-third way to Northwest River	D. v.s.	D. s.	D. v.s.	$+^{1}$
Northwest River	D.	D. v.s.	—	—
Makkovik, 30 miles north and south	D. s.	—	D. s.	—
Hopedale and 30 miles radius	D. s.	—	I. s.	—
Davis Inlet and 30 miles radius	D. v.s.	D. v.s.	D. s.	—
Nain and 35 miles radius	D. v.s.	D. s.	D. v.s.	—
Nutak	D. v.s.	s. M.I.a.	D. v.s.	—
Hebron	D. s.	I. a. M.I.a.	D. s.	—
8. Port Burwell	I. ×	D.	I. ×	0
Group 2. Coast of northern Quebec, south to Richmond Gulf and inland				
Georges River; inland and north-west to coast	D. v.s.	I. × M.I.	I. ×	0
Fort Chimo and vicinity	D. v.s.	D.	I.	—
Fort McKenzie	D. s.	D. v.s.	—	—
Leaf River and area between Koksoak River and Payne River	D. s.	D. s.	—	—
100. Wakeham Bay vicinity	D. v.s.	D. ×	D. ×	0
95. Wolstenholme Post; 30 miles east and 120 miles south	D. v.s.	D. v.s.	D. v.s.	0
101. Smith Island; inland 50 miles, south 40 miles and north 70 miles	D. v.s.	D. s.	D. v.s.	0^{2}
Povungnetuk	D. s.	D. s.	D. s.	—
Port Harrison and 70 miles radius	D. ×	I. ×	D. s.	—
40. Port Harrison and 70 miles radius	D. ×	N. ×	D. v.s.	0

Table I (*contd.*)

		Fox		Lemming		Owl		Sledge dog
	Group 3. South parts of Hudson Bay, James Bay							
41.	Belcher Islands	D.	v.s.	—		D.	s.	0
	Great Whale River and 100 miles radius	D.	v.s.	—		D.	v.s.	—
	Fort George; north, south and east, 100 miles	D.	v.s.	M.I.		—		—
	Eastmain; 50 miles coast, 200 miles inland	D.	s.	M.I.		—		—
	Rupert's House; 50 miles each side and 100 miles inland	D.		—		—		—
	Moose Factory and radius 150 miles (not mapped south of James Bay)	D.		M.I.		D.		—
	Attawapiskat and 150 miles radius	D.	s.	—		D.	s.	—
	Weenusk; 50 miles each side of Weenusk River extending 200 miles inland	D.	s.	—		D.	s.	—
	Severn and 100 miles radius	D.	s.	—		D.	s.	—
	York Factory: Hayes, Shamattawa and Kaskatawagan Rivers	D.	s.	M.I.		—		—
	Group 4. West coast of Hudson Bay							
	Churchill and 100 miles radius	D.		D.	s. M.I.a.		r.	0
21.	Outlet of Big River	N.	×		v.s.		v.a.	0
93.	Carileon Post (100 miles in an air line north-west of Fort Churchill)	D.	v.s.	—		I.	×	0
	Caribou and 50 miles radius	D.	s.	D.		N.		—
39.	58° 75′ N. to 61° N. Lat. west coast Hudson Bay. Inland roughly 150 miles to Nueltin Lake	D.	v.s.	I.	s.		×	—
	Nonala	N.		N.		N.		—
38.	Between lat. 60° and 62°, and from the coast 150 miles west	D.	×	*D.	s.	*N.	s.	—
47.	Windy Lake	N.	×	D.	s.	N.	×	0
46.	Eskimo Point, north to Dawson Inlet, south to Tha-anne River and west to Maquse Lake	D.	v.s.	I.	v.a. M.I. v.a.	I.	×	0
24.	Eskimo Point, radius 10 miles (in summer). Noonala to Tavane north and south Eskimo Point to Padley, east and west (in winter)	D.	v.s.	I.	v.a. M.a.	I.	v.s.	0
44.	Padley Post; 40 miles radius	D.	×	—			r.	0
37.	Ferguson River, Mistake Bay	D.	×		M.a.	I.	v.a.	0
94.	Mistake Bay	D.	×	I.	×	I.	×	0
	Tavane and 75 miles radius	D.		I.	M.I.	I.		—
45.	Chesterfield Inlet; and 50 miles radius	D.	v.s.	D.	v.s.	D.	v.s.	0
75.	Chesterfield Inlet south to Mistake Bay	D.	v.s.	I.			r.	0
74.	Chesterfield Inlet and vicinity	D.	v.s.	I.	×	I.	v.s.	0
76.	Baker Lake	D.	×	D.	v.s.		v.s.	0
43.	Baker Lake	D.	×	D.	×	D.	v.s.	0
83.	West end of Baker Lake	D.	×	—			r.	0
	Group 5. Southampton Island and Repulse Bay							
42.	Repulse Bay	D.	v.s.	I.	×	N.	×	0
84.	Repulse Bay	D.	v.s.	I.	×	N.	r.	0
98.	Cape Kendall. South Bay. Seahorse Point. Southampton Island	D.	×	I.	×	I.	×	0
	Group 6. Southern Baffin Island							
5.	Southern portion of Resolution Islands		s.	—		N.	s.	0
99.	Gabriel Strait to Markham Bay (by native reports)	D.	v.s.	I.	×	I.	s.	0
80.	South coast Baffin Island from Crooks Inlet to Icy Cover	D.	v.s.	I.	v.s.	I.	×	0
82.	Markham Bay	D.	v.s.		v.s.	I.	×	0

Table I (*contd.*)

	Fox	Lemming	Owl	Sledge dog
Group 6. Southern Baffin Island (*contd.*)				
97. Foxe Peninsula and country east to Amadjuak Lake and north to south end of Nettilling Lake	D. v.s.	D. v.s.	D. ×	0
96. Waddel Bay along north shore Frobisher Bay to Jordan River, thence to Newell Sound (coast)	D. v.s.	D. v.s.	r.	0[3]
81. South-east end Baffin Island from Hall Island to Cape St David, including Cyrus Field Bay, Cornell Grinnell Bay and Robinson Sound	D. v.s.	D. v.s.	I. ×	0
85. Cumberland Gulf and adjacent points	D. v.s.	D. v.s.	D. s.	0[4]
104. Cumberland Gulf	D. v.s.	*D. v.s.	D. v.s.	0
Group 7. Northern Baffin Island and north				
92. Igloolik	D. ×	D. s.	D. v.s.	0
88. Bernier Bay	D. ×	s.	D. v.s.	0
87. South end Admiralty Inlet	D. ×	D. v.s.	D. s.	0
90. East end Bylot Island and east side Baffin Island	D. ×	D. s.	D. s.	0
102. Pond's Inlet	D. ×	D. v.s.	—	0
86. Eclipse Sound (south side Bylot Island, north end Baffin Island) ...	D. ×	D. v.s.	D. v.s.	0
89. Tay Sound	D. ×	D. ×	I. s.	0
91. Arctic Bay	D. ×	D. ×	D. ×	0
103. South Coast Devon Island	D.	I. ×	—	0[5]
79. Craig Harbour District, south Ellesmere Island	D. v.s.	I. v.s.	—	0
Group 8. Boothia Peninsula and islands west				
31. King William Island south portion of Boothia Peninsula. Adelaide Peninsula	D. v.s.	D. v.s.	D. v.s.	*+[6]
33. King William Island, Adelaide Peninsula, Boothia Isthmus and vicinity	D. v.s.	D. v.s.	D. v.s.	*+[7]
120. Cambridge Bay west to Wilmot Island, east to King William Island ...	D.	N. r.	N. s.	*+[8]
34. Richardson Island, west 50 miles to Lady Franklin Point, east 50 miles and native reports on Victoria Island	D.	D. ×	D. s.	+[9]
71. Reid Island, south to Bernard Harbour, east to Lady Franklin Point, west to Williams Point, north to north shore of Prince Albert Sound	I. ×	I. ×	I.	0
36. 50 miles west of old site of Fort Brabant. Trap-lines east and west 20 miles along the coast from this point	D. v.s.	D. v.s.	D. v.s.	0
105. Walker Bay district north to Deans Dundas Bay, south to Minto Inlet ...	D. ×	I. ×	D. v.s.	0
Group 9. Adelaide Peninsula west to Coppermine and inland to Aylmer Lake				
31. Adelaide Peninsula (see also above) ...	D. s.	D. v.s.	D. v.s.	+[6]
33. Adelaide Peninsula (see also above) ...	D. v.s.	D. v.s.	D. v.s.	+[7]
70. Bathurst Inlet, both shores; inland from south and south-west 100 miles; from east 35 miles	D. ×	I. a. M.I.a.	r.	0
13. Wollaston Point	D.	v.s.	r.	0
76. 50 miles radius Kugaryuak (45 miles east Coppermine River)	D. s.	D. s.	D. s.	0
14. East of Red Rock Lake	D. v.s.	r.	—	—
15. Back River District from Musk-ox Lake to Fry Lake and Beechy Lake district	I. ×	I. s.	D. ×	0
†**16.** North of west end of Aylmer Lake ...	N. s.	N. s.	N. s.	*0

† One sledge dog symbol used for both **16** and **68.**

Table I (*contd.*)

	Fox	Lemming		Owl	Sledge dog
Group 10. Dubawnt Lake, west to Fort Rae and Fort Resolution					
9. Carey Lake, north-east to Dubawnt Lake	D. v.s.	—		r.	—
25. From Lake Eileen east to within 50 miles of Dubawnt River	D. v.s.	*N. a.		v.s.	*0
22. Lynx Lake district. Headquarters of Thelon River	D. v.s.	I. ×		r.	0
23. East of north end Whitefish Lake	D. ×	r.		N. ×	0
52. South end Artillery Lake, east to Tent Lake	D. v.s.	I. s.		D. s.	+[10]
†**68.** Ptarmigan Lake and Clinton Colden Lake	D. v.s.	I. ×		N. s.	0
53. Snowdrift River to Nonacho Lake district	D. v.s.	—		N. r.	+[11]
64. Snowdrift and 50 miles radius	D. v.s.	—		—	0
Rocher River	D.	—	M.I.a.	D.	—
6. La Loche River	D. v.s.	—		D. v.s.	+[12]
50. Resolution east to Taltson River, up Taltson River to Slave River across country to Little Buffalo River, thence down to Great Slave Lake	r.	—		N. r.	0
Fort Rae, south-east 100 miles; east 150 miles; north 200 miles; west 25 miles; north-west 150 miles	D. s.	r.	M.I.a.	I. a.	0
Group 11. From Coppermine River to Alaska					
32. Coppermine River from Coppermine settlement to Bloody Falls (12 miles) and region 5 miles east and west of settlement	D. v.s.	I. a.		D. v.s.	+[13]
Fort Hearne and 5 miles east and west of Coppermine	D. s.	D. s.		—	—
35. Rae River and west on tributary about 75 miles from mouth, then on land for 50–60 miles west to north-west	D. v.s.	I. ×		—	0
11. Bottom of Darnley Bay to Toukturiaktuk (coast)	D.	—		N.	0
4. Langton Bay to Pearce Point. (For fox: Langton Bay, N.; Darnley Bay, D.)	D. × N. ×	—		D. s.	*0
69. Letty Harbour	N. ×	N. ×		I. ×	0
Baillie Island and 50 miles radius	D.	I.		D.	—
116. Baillie Island east to Pearce Point and west to Richards Island (coast)	D. v.s.	*D. v.s.		N. ×	0
58. Aklavik north to mouth of Mackenzie River, and west to Herschel Island and east to Atkinson Point	D. s.	* v.s.		* v.s.	*0
117. Mackenzie Delta (lower end)	I. ×	—		D. v.s.	0
Aklavik and lower delta of Mackenzie River	D. s.	D. ×		D. ×	—
14. Herschel Island. From Shingle Point, Yukon Territory, to Demarcation Point	D. s.	D. s.		D.	—

† One sledge dog symbol used for both **16** and **68**.

Table 2. *State of arctic fox, lemming and snowy owl populations in* 1935–6

Heavy type = number of observers. Ordinary type = number of arrows. Group numbers are given in the maps and described in Table 1

Group No. ...	1	2	3	4	5	6	7	8	9	10	11	Total	%
Arctic fox													
Increase	**1** 1	— —	— —	— —	— —	— —	— —	**1** 3	**1** 1	— —	**1** 1	**4** 6	**4** 3
Decrease	**10** 10	**10** 15	**10** 43	**17** 29	**3** 6	**8** 25	**10** 15	**6** 8	**4** 10	**11** 19	**9½** 13	**98½** 193	**91** 95
No change	— —	— —	— —	**3** 3	— —	— —	— —	— —	**1** 1	— —	**1½** 1	**5½** 5	**5** 2
	11 11	**10** 15	**10** 43	**20** 32	**3** 6	**8** 25	**10** 15	**7** 11	**6** 12	**11** 19	**12** 15	**108** 204	**100** 100
Lemming													
Increase	**1** 1	**2** 4	— —	**7** 17	**3** 6	**2** 6	**2** 5	**2** 4	**2** 6	**3** 3	**3** 5	**27** 57	**37** 41
Decrease	**5** 5	**7** 11	— —	**7** 16	— —	**5** 19	**7** 9	**4** 5	**1** 3	— —	**4** 4	**40** 72	**55** 53
No change	— —	**1** 3	— —	**1** 1	— —	— —	— —	**1** 1	**1** 1	**1** 1	**1** 1	**6** 8	**8** 6
	6 6	**10** 18	— —	**15** 34	**3** 6	**7** 25	**9** 14	**7** 10	**4** 10	**4** 4	**8** 10	**73** 137	**100** 100
Snowy owl													
Increase	**2** 2	**2** 2	— —	**7** 12	**1** 4	**4** 6	**1** 1	**1** 3	— —	**1** 9	**1** 1	**20** 40	**25** 25
Decrease	**8** 8	**6** 9	**6** 33	**2** 4	— —	**3** 15	**6** 10	**5** 7	**2** 4	**3** 2	**6** 8	**47** 100	**57** 64
No change	— —	— —	— —	**4** 4	**2** 2	**1** 1	— —	**1** 1	**1** 1	**4** 4	**2** 5	**15** 18	**18** 11
	10 10	**8** 11	**6** 33	**13** 20	**3** 6	**8** 22	**7** 11	**7** 11	**3** 5	**8** 15	**9** 14	**82** 158	**100** 100

Table 3. *Details of disease among sledge dogs*, 1935–36

Numbers indicate that the full description of an area has already been given and is to be found opposite the corresponding small number in the last column of Table 1.

(*a*) *Disease or epidemic prevalent* ("Yes" to question 2; + on map).

1. *Rigolet.* "A few cases of disease" (attributed to starvation following seal scarcity).

6. *King William Island and Adelaide Peninsula.* "Disease started in October and became epidemic, finally disappearing in Feb. There was a tendency to quarrel and fight; irregularity of movements of the limbs, causing sideways staggering when walking. Finally paralysis, snapping of the jaws and foaming at the mouth, followed by death. All dogs were suffering from malnutrition and even starvation early in the fall owing to the scarcity of game, the natives being unable to feed them from the scanty reserves they had on hand for their own use during the dark period. In these circumstances the disease became evident and did not disappear until February, when seals became more plentiful and surviving dogs were properly fed."

7 and 8. Confirm 6.

9. *Richardson Island.* "From September to April there was distemper and lameness in hind legs. Some go crazy and have to be shot—foam at mouth and wet coat. Mostly young dogs affected."

10. *Artillery Lake, south end.* "Foaming at mouth, act crazy, die in harness although in good condition. January."

Snowdrift River, north to Yellowknife Preserve and east to Artillery Lake. "Pus coming from nose and eyes; weak back, loss of appetite, sneezing, drying up of nose, fast breathing. May."

11. *Snowdrift.* "In May and June (? 1936) symptoms: sometimes cramps, blood from mouth, act crazy, finally die."

Fort Smith district and in the districts of Lady Grey Lake, Hill Island Lake, Thekulthili Lake and Nonacho Lake which are north-east from Fort Smith. (Epidemic in Dec. 1935 and Jan. 1936; respiratory symptoms.)

Fort Smith. "Distemper occurred about the New Year. Of my own dogs, three took sick in middle of February. One recovered in 6 weeks; two still sick, 10th June 1936."

12. *Fort Resolution.* "Distemper, pneumonia, worms, short and long tape worms. Jan. to July 1935."

13. *Coppermine.* "Believed to be a form of distemper. This was among young dogs (under 1 year) and pups. Dogs refused to eat, seemed listless; second and third day seemed to lose use of hind legs. Some vomited, others tried without success. Pup of seven weeks also had above symptoms and finally on fourth day went crazy and tried climbing walls, etc. All young dogs and the pup died within a week. One dog got mange in Jan. All dogs have been well fed."

Peel River. "Quite a number have died in last two years (January 1935; February 1936) both here, at Aklavik and Old Crow." (Paralysis of legs noted.)

Thunder River. "December, 1935. A few deaths: bluish discharge from mouth and nostrils." (This is the only positive report of many from surrounding districts.)

Norman. "Epidemic not general but occurred in a hit and miss manner (November and December 1935). Symptoms: fever, lack of appetite, occasional discharge at eyes and nose, closing of the bronchial tubes, fits sometimes evident and at others a kind of drunken stupor. Thought to be distemper." (But pathological tests inconclusive.)

Norman. "Distemper in March and April."

Norman. "Distemper epidemic in April, May, June 1935. 20% died."

(*b*) *Isolated cases of disease* ("No" to question 2, but qualified as below; o on map).

2. *Smith Island.* "Disease in one dog only—swelling in the throat accompanied by noisy and stifled breathing. Early November."

3. *Waddel Bay.* "No epidemic, but a few cases of scabies; running sores and loss of hair. This was observed to a slight degree all the year round but mostly in late summer and early fall."

4. *Cumberland Gulf.* "Dogs in this area have been pretty well free from serious epidemics or disease this past year; only isolated cases have occurred. In Pangnirtung a slight outbreak occurred in Sept., Oct. and Nov.... Three dogs were affected; one died, one was destroyed, one recovered. Disease had the symptoms of distemper. The eyes were gummed, while a thick yellow fluid issued from the nostrils. Breathing at times was slow and stertorous."

5. *Devon Island.* "Sickness not prevalent. One dog died in May 1936 with paralysis of the legs, accompanied by great weakness and foaming at the mouth."

Great Slave Lake, south and west shore. "Nothing out of the usual distemper although it was more prevalent than last year."

(*c*) *Disease absent* ("No" to question 2; o on map).

Fort Providence, Hay River and districts. *Cameron Bay Settlements*, Great Bear Lake, and 100 miles radius. *Hornby Bay*, east Great Bear Lake. *Coppermine River* mouth. *Fort McPherson; Peel River Preserve*, Fort McPherson. *Point Separation* (omitted from map). *Arctic Red River*

Settlement (two observers). *Thunder River*, 12 miles down river from; *Thunder River*, 80 miles south-east of Arctic Red River; *Thunder River* and Mackenzie River, within a radius of 10 miles; *Tutsieta River*, 20 miles north of, on the Mackenzie and within a radius of 10 miles. *Arctic Red River Settlement*, south along left bank of Arctic Red River to intersection with 66th parl. N. lat. *Trail Creek* off Peel River, McPherson district. *Gillis River*, 12 miles north of, (lat. 66° 43′ N.; long. 129° 49′ W.); *Gillis River*, south of. *Fort Good Hope* (two observers). *Fort Wrigley* and Mackenzie River valley south to Willow River, north to Blackwater River. *Nahanni River* mouth, 6 miles each way up and down Mackenzie, 25 miles south along Nahanni, 50 miles south-east along south branch of Nahanni, 5 miles inland along this route. *Liard River*. *Nahanni River* mouth.

5. Summary

1. The Northwest Territories Administration of the Canadian Government has initiated an annual questionnaire enquiry into the fluctuations in numbers of the arctic fox (*Alopex lagopus*), lemmings (*Lemmus* and *Dicrostonyx*), snowy owl (*Nyctea nyctea*), and ptarmigan (*Lagopus*), and epidemic diseases among sledge dogs, in the Canadian Arctic. The Hudson's Bay Company co-operated in supplying information.

2. 163 reports fort he season 1935–36 were received and the results mapped in the Bureau of Animal Population at Oxford.

3. Observations are made on a comparative basis from year to year. The results are mapped by a method which allows for differences in the areas covered by observers, and combines all types of record on to a single map for each species.

4. Arctic foxes showed almost universal decrease and scarcity. More than a third of the observers reported increase in lemmings: increase in snowy owls was also reported from some of the same points. The ptarmigan data are reserved for future publication.

5. There were practically no reports of disease among sledge dogs in the Eastern Arctic, and only a few on the Western Arctic coast and islands. Disease was reported more frequently from the Great Slave Lake area and a few other points in the Mackenzie River Valley.

6. These fluctuations are a vital factor in the economy of the Canadian Arctic, since they affect the fur trade, food supply, and dog transport. The enquiry is being continued.

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REVIEWS

THE AUGUST ISSUE OF *THE JOURNAL OF ECOLOGY*
(Vol. 25, No. 2, 1937)

The last issue of the *Journal of Ecology* contains 12 original papers, including a short note on the dispersal of ragwort. An unusually large proportion is devoted to aquatic ecology. The two longest papers are a fully illustrated account of the vegetation of Mauritius by Messrs Vaughan and Wiehe, an admirably thorough and careful piece of work with vegetational and topographical maps; and an ecological and taxonomic investigation of the littoral algal flora of Lake Windermere by Miss M. Godward, supplementing Dr Pearsall's studies of the macrophytic aquatic vegetation and of the phytoplankton of the English lakes published in the *Journal* in 1920 and 1932 respectively. Both these papers are models of what such work should be. A shorter paper on microscopic freshwater vegetation is Dr Mary J. Reese's study of the effect of pollution from the lead mines on the microflora of the Rheidol and Melindwr in Cardiganshire. A strikingly original and illuminating paper is Mr Picken's "Structure of some Protozoan communities", which considers the factors moulding the "biotic communities" of algae and protozoa found in the headwaters of the Cam at Ashwell. Three papers are concerned with seaweeds: Part 2 of Anand's ecological study of the algae of the British chalk cliffs, which deals experimentally with the ecological factors differentiating the communities described in Part 1; Kitching's investigation of recolonization of denuded areas, previously populated by *Corallina*, at the upper margin of the sublittoral zone on the coast at Wembury Bay, S. Devon; and Zaneveld's very interesting study of the factors causing the zonation of the communities of Fucaceae on the "Leidam" at Den Helder in Holland, the author showing that desiccation is much the most important of the determining factors, and achieving a greater accuracy than any previous worker in fixing periods of exposure in relation to tide levels.

Other papers are H. Baker's comparative study of very old alluvial meadows at Oxford in which he shows the profound differential effects on the meadow flora of long continued grazing on the one hand and mowing on the other; a short preliminary note on the mycorrhiza of beech by J. L. Harley, in which he distinguishes several form-types of mycorrhiza, and shows that the size and vigour of beech trees on the Chilterns depends more upon soil type than on fungal infection, and that if fungal infection increases the supply of nitrogen to the beech it does not overcome the differences in supply due directly to the low nitrogen content of the highly acid podsols; a study of the induced plant communities of wayside and hedgerow by G. H. Bates; and an interesting general paper on the effect of sheep on the vegetation of Scotland by E. Wyllie Fenton.

Professor Tansley, who has edited *The Journal of Ecology* for 21 years, is now retiring in favour of Dr W. H. Pearsall of Leeds University.

A. G. T.

A LOCAL NATURAL HISTORY SURVEY

W. M. Tattersall (editor) & others (1936). *Glamorgan County History. Vol. I. Natural History.* xix+444 pp.; 27 text-figures, 40 plates and 4 maps. William Lewis (Printers), Ltd., Cardiff. Price 25*s*.

There are few more fruitful ways of promoting the study of natural history than local surveys and the making of local lists. The catalogues themselves may serve little else than our knowledge of geographical distribution but a great deal of biological and ecological information is accumulated in their making, and their publication is always an effective stimulus for further work in the neighbourhood as well as of interest to those more familiar with other districts.

The gang of specialists gathered together by Prof. Tattersall here surveys the geology, botany and zoology of Glamorgan, a varied and attractive county which has in parts been substantially changed by intense industrialization: with the exception of the seaweeds and birds marine life seems to be omitted. On the whole the result is excellent though there is, perhaps inevitably, great variation in different sections: the only serious complaint is that the entomologists have not been made to disgorge some of the wealth of ecological knowledge which they must have and which they always seem so reluctant to put into print.

The other major sections are more satisfying and there are many items of interest, e.g. that ravens and peregrines have borne the urbanization of the northern valleys better than the buzzards which have practically disappeared, or that *Plusia moneta* flourishes on its natural food plant monkshood where this grows, apparently wild, along the river near Bridgend. The plant ecology is also treated systematically.

The printers have produced the work in a handsome quarto which is no doubt an ornament to any gentleman's library. But it weighs about 5½ lb. and is for practical use very inconvenient: the working naturalist would have done better with a modest octavo, smaller type and less ample margins. The index too is far from satisfactory: there is for instance an interesting question whether the beech is native in the county, which is referred to at least three times in the text (though not in the chapter headed "Trees and Shrubs") and occupies a plate, but neither "beech" nor "*Fagus*" occur in the index. Some of the illustrations, such as the photographs of snakes, are of no local interest and could well have been replaced by more pictures of characteristic scenery and habitats.

But with so much that is good it is ungrateful to pick holes in a book which we all wish could be repeated for every county. And at its reasonable price it ought to be read widely and with profit: the botanical information given about the tarns on Craig-y-Llyn has already led to the discovery of *Pisidium lilljeborgii* in its furthest south locus in Great Britain.

A. E. BOYCOTT.

INTERTIDAL SURVEYS

(1) **Holger Madsen (1936).** *Investigations on the shore fauna of East Greenland, with a survey of the shores of other Arctic regions.* Meddelelser om Grønland, 100, No. 8: 1–79.

(2) **Willis G. Hewatt (1937).** *Ecological studies on selected marine intertidal communities of Monterey Bay, California.* American Midland Naturalist, 18: 161–206.

(1) A description is given of the results of a series of collections from the intertidal and drift line zones between latitudes 70° 29′ and 74° 05′ N., made in the summer of 1933 with Dr Lauge Koch's "Three Year Expedition". The fauna of this area is very poor in species, owing to the high Arctic conditions and to the short period of the year during which the coast is free from ice. Most of the observations were on different types of sediment, and on these the typical fauna consisted of two or three species of Turbellaria (*Notokaryoplana arctica* and *Monocelis fusca*), Enchytraeid worms (*Enchytraeus albidus*, *Lumbricillus lineatus*), an occasional Nemertine or Polychaete, and a few species of Crustacea (3 species of Harpacticoidea, *Gammarus wilkitzi*, *Pseudalibrotus littoralis*, and occasionally *Mysis oculata*). Chironomid larvae, Infusoria, small Nematodes, and Flagellates were also found at some stations. Mollusca were completely absent, as were also Coelenterates, Echinoderms and Chordates (except for small fish, *Cottus* sp., at one station).

The latter part is a comparison with the fauna of West Greenland and other Arctic regions, and a discussion on the definition of zoogeographical limits in this field. It is proposed to distinguish only a true Arctic and a Boreo-Arctic zone, in contrast to the Russian workers (Gurjanova and others) who have described three. The southern boundary of the true Arctic is defined as the northern limit of littoral Mollusca and of the barnacle *Balanus balanoides*; and of the Boreo-Arctic by the southern limit of two typically Arctic species, *Pseudalibrotus littoralis* and *Mysis oculata*. The distribution of these species is discussed,

and it is suggested that a study of their limits on the west coast of Greenland would be important with a view to testing their usefulness in this respect.

(2) A description is given of the occurrence and distribution of 90 species of animals found on a shore transect over a period of 21 months, in order to determine the nature and causes of the vertical and horizontal zonation of the intertidal fauna. A single transect was 108 yd. long, and was investigated in 1 yd. squares, the position of each relative to the vertical tide scale being accurately determined. It was so chosen as to include representative areas of all types of rock shore—sheltered, exposed to surf action, and rock pool.

During the experimental period a close study was made of the environmental conditions, including complete records of the water temperature and salinity, rainfall, the phosphate and silicate content of the water, the light intensities, and the height of the tides. These show an extreme monotony of physico-chemical conditions: for instance an average annual range of temperature at the surface of 2·5° C. and a salinity variation of only 32·12–33·82 g. per l.

It is claimed that there is a definite zonation of the intertidal fauna, with three distinct zonal limits. The one at mean low-water mark (0·0 ft. on the map levels) was the most definite, being as in Colman's observations on Church Reef near Plymouth the upper limit of many subtidal species. The other two limits, between the 2 and 3 ft. levels and at 5 ft. respectively of an 8 ft. tide range, were less definite, though they are believed to be correlated with the relative lengths of the periods of exposure to desiccation. Very complete tables are given of the number of species found, of their distribution at the different levels, and of the number of species for which each level is a limit. In addition there is a valuable discussion of the ecological relationships of the fauna in terms of relative numbers and food supply.

The value of this method of attempting to demonstrate zonation is open to doubt, since it is based on a single count only of each square on the transect. Also the dates of the counts are not given, and no indication that recounts of the same squares were made, thus not eliminating the possibility of seasonal migration of species to different levels on the shore. Until such work has been done, claims to have established limiting zones controlled by definite factors cannot be unreservedly accepted.

D. M. STEVEN.

WILDLIFE PROBLEMS IN NORTH AMERICA

Wildlife restoration and conservation. Proceedings of the North American Wildlife Conference called by President Franklin D. Roosevelt. 1936. 675 pp. U.S. Govt. Printing Office, Washington, D.C.

When a wildlife conference is summoned by the President of the United States, managed by some of the world's most able conservationists and attended by a cross-section of public opinion from senators to boy scouts, one realizes that the American capacity for organization is likely to be a powerful weapon in the fight for wildlife conservation.

There are in the United States over 400 million acres under administration by the Federal Government on which it has no jurisdiction over animals other than migratory birds; some 12–15 million dollars annually are spent under chaotic and technically inadequate supervision; 100 million acres of original wildlife breeding grounds have been drained (half of them uselessly); 85% of the lakes and streams are polluted; erosion is proceeding at a rate of 250,000 acres a year. These are some of the gloomy facts heard by representatives of the United States, Canada and Mexico.

At this 5-day conference active measures were taken for the federation of the various wildlife interests in order to forward the vital need for a nation-wide programme of wildlife conservation. It is obvious that while there is a large body of enlightened opinion there has been a lack of means of exerting its power or of spreading its knowledge. For example a mere $35,000 annually would be enough to reach an audience of 30,000,000 every day — through proper wildlife education in the schools.

Wildlife is recognized as one of the valuable resources of the national forests and the creation of a Division of Wildlife Management in the Forest Service is now announced.

Adequate forest management as practised in the national forests encourages wildlife just as surely as private forest exploitation depletes it: and 80% of all forest land is privately owned. There is insufficient winter range in the national forests and game is forced to run the dangers of moving on to privately owned lands for part of the winter. In the national parks all forms of wildlife receive complete protection. However, it will be impossible to perpetuate those species threatened with extinction without a wide national programme to cover areas outside the parks.

The activities of the Soil Conservation Service offer magnificent opportunities for the resoration of wildlife to denuded areas. "Soil conservation means wildlife conservation", and to realize this a Section of Wildlife Management has newly been established. In selecting plants for soil stabilization those species are chosen that are most suited to wildlife requirements. These projects are carried out in co-operation with farmers who, at the end of 5 years, are expected to have become sufficiently interested to continue on their own.

The important key-position held by the farmer is fully realized and several farmer-sportsman co-operative schemes are being tried out. In this and in other aspects of wildlife management the universities are carrying out important programmes of work.

Referring to the work of the Bureau of Fisheries Mr Frank T. Bell said: "Most of the ills of the commercial fisheries may be traced to the lack of knowledge concerning fluctuations in abundance of the supply...a huge economic waste [is] occasioned by unforeseen gluts and famines....Recent scientific work has proven that these vast variations in supply in some of our most important fishes can be foreseen....Much scientific knowledge is yet to be acquired and much experience to be gained before predictions of future yields can be entirely reliable, but the goal is worth untold effort."

It is impossible to mention more of the many excellent papers dealing with the steps it is proposed to take and with those already in operation by federal, state, university and private organizations. However, these measures will have to stand the test of a situation the seriousness of which was summed up as follows by Prof. William T. Hornaday: "...this conference is in practical effect and virtue the last call for the protection and restoration of the small game of the United States and Canada....It is time for the last follies and crimes in game slaughter to be sternly thrust aside before it is utterly too late to save the breeding stocks of game...."

DENNIS CHITTY.

BIG GAME MANAGEMENT

J. Stevenson-Hamilton (1937). *South African Eden. From Sabi Game Reserve to Kruger National Park.* 311 pp. and 25 illustrations. Cassell and Co. Ltd., London. Price 12*s.* 6*d.*

It is a strange but almost invariable rule that wherever someone first undertakes a really constructive programme relative to wildlife he becomes the immediate victim of obstructionist forces. There are people who think their interests will be harmed, unsympathetic government officials, and an apathetic or ignorant public. The lesson from the Kruger National Park, for 35 years under the wardenship of Lieut.-Col. Stevenson-Hamilton, is that once ignorance can be dispelled, administrative obstacles become considerably fewer.

This book is a thoroughly entertaining account of the development of a huge National Park and of the growth of the public conscience that accompanied it. Nineteenth-century sporting ethic permitted one to boast of the numbers of animals merely wounded; natives shot and snared unchecked, and military, prospecting and constructional camps "lived off the land." The early efforts of the warden to preserve the fauna for itself and not as a future target were variously called "queer hobby", "public scandal" or a waste of good land.

Although the book is not intended to be a scientific treatise upon game management, it contains a great deal that will interest the professional biologist. As a result of the author's energetic policing of the reserve, game has increased from near extinction to great abundance. Up to 1926, when the Sabi Game Reserve became the Kruger National Park, it was thought necessary to try to control the numbers of lions (partly on account of outside criticism),

and also hunting dogs, reptiles and to some extent raptorial birds. It is particularly interesting that the author ascribes little or none of the game increase to the effects of this policy.

When lions were continually hunted, their rate of increase was great and it was almost impossible to keep their numbers static; but when shooting ceased competition for food, particularly between the young and the old, became a far more efficient limiting factor to the density of game. In the northern portion of the reserve, where for 30 years almost no artificial checks were placed upon the increase of carnivores, eland and nyala increased from apparently *nothing* to great abundance. To-day lions are the greatest attraction of the park, and since they are no longer molested, they have adopted a diurnal habit and may be seen sleeping, playing or pulling down their prey in broad daylight.

Wild dogs (*Lycaon pictus*), despite vigorous persecution, were only partially reduced from their high abundance of 1902 until in recent years they decreased, apparently from domestic canine distemper. As a consequence their chief prey, impala, have in places now eaten themselves out of food supplies and spread into habitats formerly believed unsuitable. Reedbuck, on the other hand, for whose virtual disappearance misinformed amateurs blamed the wild dogs, decreased from abundance in 1902 to scarcity ever since 1916.

Appointments to the staff and to the Board of Control are outside the realm of politics, a feature in which this park is fortunate. At present the requirements of the tourist traffic place a very heavy strain upon the staff and it is to be hoped that this will not prevent the development of scientific work, of the vast possibilities of which the present warden if fully conscious.

DENNIS CHITTY.

THE INHABITANTS OF TREES

(1) **R. Neil Chrystal (1937).** *Insects of the British woodlands.* 338 pp. and 33 plates and figures. Frederick Warne and Co., Ltd., London and New York. Price 7*s.* 6*d.*

(2) **A. M. Massee (1937).** *The pests of fruits and hops.* 294 pp. and 26 plates. Crosby Lockwood and Son, Ltd., Stationers' Hall Court, London, E.C. 4. Price 15*s.*

(1) This is an important work of reference, which originated as an instruction manual for a forester's training school, and therefore contains a certain amount of elementary entomology as well as the main subject matter. It gives very clear descriptions of all the insects which ever become pests to forest trees in this country, with suggestions for their field study and elaborate guides to their classification. Besides accounts of the well-known pests (which are mainly Aphids, moths, beetles, sawflies and gall midges) and a few of their parasites, there is one appendix giving descriptions of a number of common forest beetles and a few other insects, and another containing a classified list of all the important or potential pests and the trees they frequent.

It is obvious that no one working on woodland ecology can possibly afford to be without this book, which is the result of much patient and thorough work, and is excellently illustrated by line drawings of the insects, and photographs of damage done by them. There is also an adequate, and not too long bibliography.

The chief criticism that an ecologist will make is that the title of the book is misleading, since there is no idea in it of giving a complete account of the insects that live in British woodlands. It may be answered that such a task is at present impossible to accomplish, and that is true. But it would have been more correct to call it the "insect pests of British woodland trees." The assemblage of insects and other animals in our woodlands runs into many thousands. However, the author is certainly justified in tackling one phase at a time of this huge field, and ecologists will be grateful to him for writing such a competent guide book.

The next step is to find out how many and what species inhabit British trees *without* doing them any harm: the relative abundance in individuals and species of pests and non-

pests in a given animal community is a subject of great interest about which little is ascertained.

(2) The study of fruit tree pests forms the natural counterpart to that of forest pests, and the ecological methods of approach are identical, although control methods differ in their scale, dependent upon the smaller areas of orchards. This book is admirable in its printing, arrangement, and illustrations. It should be possible for both the working ecologist and the amateur naturalist to identify and learn something about almost any common vegetarian insect inhabiting fruit trees. There is also an equal amount of information about fruit-shrubs, strawberries, and hops. Of particular interest to animal ecologists are the carefully arranged lists of the species that attack or at any rate live on each fruit tree or shrub. Here are some of the numbers: apple, 75; plum and damson, 55; cherry, 34; pear, 19; gooseberry, 19; hop, 15. Many of these species (which are practically all insects, and mostly beetles, moths, sawflies, flies, Aphids and bugs, with a few mites) come on more than one fruit plant. There is a great deal of ecological information packed in here, including notes on natural enemies, and some curious interrelations. The most interesting of these is the case of the fruit tree "red spider" (*Oligonychus ulmi*)—a mite which lays red eggs on apples, plums and damsons. This mite was formerly controlled naturally by predaceous Anthocorid bugs, which are, however, easily killed by the modern tar distillate sprays, while the eggs of the mite are not. The result has been the emergence of a new pest. There is, of course, a great deal of information about practical measures of control, which has authority behind it, since the author is on the staff of East Malling Research Station in Kent. There is also full reference to literature.

CHARLES ELTON.

MICROCLIMATES AND FROST

W. R. Day & T. R. Peace (1937). *Spring frosts.* Bulletin of the Forestry Commission, London, No. 18. 131 pp., 23 photos. H.M. Stationery Office, London. Price 2*s.* 6*d.*

Many people will remember the brown beeches and blackened oaks and ashes that were left after the late frosts of 15 and 17–18 May 1935; although it was the wide occurrence rather than the severity of the frosts that made them so remarkable.

Spring frosts are quite common in Great Britain, as the authors show, and are liable to happen up to about 20 May in any year. They are one of the anxieties of the forester, especially in young plantations and nurseries. But they also form a critical feature in the seasonal variations of vegetation generally, and of the animal life dependent upon it. Although this report does not mention the influence of frost on animals, e.g. upon the course of development of pest insects and their parasites, the connexion must be an important one for study.

The work done at Oxford upon this problem dates back to earlier severe spring frosts in 1927 and 1929, which underlined its importance to forestry work; and the report therefore represents a long piece of research, brought to a head by the events of May 1935. May is the time when buds have burst or are beginning to do so, and serious frost at once shows which species are hardy, and which of those are not, but develop late enough to escape damage.

The distribution of frost according to climate and the nature of the ground forms perhaps the most interesting part of the report. Cold air, dependent for its formation upon the general weather conditions (i.e. whether cold winds are blowing and whether there is a clear sky and so on), flows like water down hill, and collects to form invisible pools and lakes of different depths. This takes place especially at night. The shape of the ground forms one obstacle to flow, and the nature of the vegetation—as young trees closely set—another. The authors point out the importance of planting shelter belts up and down hill and not across, in order that the cold air shall not bank up against them. The study of different shapes of country and their relation to the incidence of frost encourage the authors to speak of the May 1935 frost as a "blessing in disguise", since it formed a natural experiment which it is unlikely we can ever imitate by growing forests in refrigerators!

Although the effects of this frost could be found in almost all regions of Great Britain, they were unevenly distributed. The South-West escaped lightly, as did the North Midlands. A good map is given, filled with a large number of reports from the Forestry Commission's men, from an enquiry in the *Times* and from personal visits.

Some species were hardly touched at all. These included the cypresses, juniper, Scot's pine, maple, horse chestnut, birch, hornbeam, hazel, willows, privet, poplars, *Prunus* and *Pyrus*. Elm, lime, hawthorn, and larches suffered much less than other trees, though local damage occurred. The worst effects were seen on Sitka spruce, the early flushing races of Norway spruce, Douglas spruce (though not much in Scotland), sycamore, sweet chestnut, beech, ash, oaks, and walnuts. One feels that Darwin would have taken particular pleasure in reading such concrete (and well arranged and documented) evidence of the struggle for existence among plants in this country at the present day.

C. E.

L. W. Hackett (1937). *Malaria in Europe: an ecological study.* 336 pp. and 60 figures. Oxford University Press. Price 10*s.* 6*d.*

This is an extremely interesting and readable account of the triangular relationships between the malaria parasites, the mosquitoes which carry them and man. Theoretically the control of human malaria is as easy as could be; in practice it has proved very difficult and the disease still remains one of the major scourges of the world. The difficulties have arisen because the original conception of what happened was much too simple and the more the facts are investigated the more complicated they prove to be; whether they are studied in the field or by the experimental inoculation of human beings in the treatment of general paralysis.

There are perhaps four or five species of parasite which may be distinguished by morphological differences and within these are various races which vary in their habits in mosquito and man. Scattered over the world there are about a dozen anophelines which are important vectors and here again within a morphological species are a number of subspecies, races or groups which have their own particular habits and preferences that turn out to be of the first importance when their control is attempted. Least of all is the life of the parasite in man understood, especially with regard to the conditions which lead to the presence in the peripheral blood of the sexual forms that alone can infect the mosquito and on which the continuance of the cycle depends.

Apart from its technical interest, the book is of general importance because it brings out so clearly the necessity of taking into ecological account such characters as habitats and habits as well as the utmost refinements of the taxonomists.

A. E. BOYCOTT.

SHORT REVIEWS

Various authors (1937). *St Kilda Papers* 1931. Oxford University Press. (Not on sale.)

A collection of papers already published by J. N. S. Buchan, T. H. Harrisson, D. Lack, J. A. Moy-Thomas, C. P. Petch, M. Stewart, members of the Oxford and Cambridge student expedition that carried out surveys in 1931. They deal with the St Kilda mice, birds, insects, and a plant ecological survey. The new matter consists of a brief introduction describing the expedition, and the history of the island since the expedition went there. (The comment on St Kilda's present status and the prospects of ecological work being continued is discouraging.) There is also a very complete bibliography of all references to St Kilda, and a copy of the O.S. 6-in. map. The volume has been published in a limited edition not placed on the market, but copies have been presented to 25 of the chief libraries (general and scientific) in Great Britain, though apparently not to any abroad. It forms a very useful record of previous work on the island, and of the 1931 survey done just after the evacuation of the inhabitants. Let us hope that there will be another survey in 1941.

C. E.

R. Bracher (1937). *Ecology in town and classroom.* 96 small pp. and 9 figures. J. W. Arrowsmith, Ltd., 12 Small Street, Bristol, 1. Price 2*s.* 6*d.*

Following upon her earlier book which gave examples of some "natural" plant communities, and simple methods for their study, Miss Bracher has now written a short account of some plant communities found in towns, which can be used for study by town schools. These studies are all based on actual examples, and they include streets (the author speaks rather regretfully of the cleaning of the town square in Salisbury and of the decrease in the flora of Piccadilly); waste ground such as building sites, neglected gardens, etc.; coal tips; marshy ground; and tidal river banks. Her reason for omitting the flora of parks and gardens seems to be that in them ecological succession does not go on in the same (by man) uncontrolled manner as in the other habitats. And yet there must be many opportunities for working in such places. There are some clear notes and suggestions for the methods of survey. It would be easy to work out a few ways of combining animal observations with such plant ecology, especially as the communities are rather poor in species—always the dream of the animal ecologist engaged upon survey-work.

C. E.

The Journal of Wildlife Management. Vol. 1, Nos. 1 2: pp. 1–47. The Wildlife Society, 450 Ahnaip Street, Menasha, Wisconsin, U.S.A. Subscription 3 dollars p.a., single copies 75 c.

A few years ago Prof. Carr-Saunders made a special study of the means by which various professions have been able to raise and maintain high standards of performance and integrity, and he was able to prove beyond any doubt the great influence that professional societies and unions have had on the growth of independent, fearless criticism, and the introduction of improved technical education to meet particular needs. The Wildlife Society has been started in the United States to bring together people who are actively interested in conservation, wildlife management and restoration, and game and fish management, and the *Journal of Wildlife Management* has as its aims the encouragement of reliable research and first-rate practical measures.

There is a refreshing frankness and vigour in the statements of policy printed in this first number, and the names of those in charge encourage one to hope that their ideals will be maintained in the future. A significant remark is that "speculations, prophecies, or accounts of untried plans will in general be eschewed".

The first number has obviously been produced under some pressure, but contains some useful ecological research on nesting mortality in wild pheasants and its effect on the year's stock; 7 years' experience of the quantity of fur produced by a small farm area; the influence of game refuges on the preservation of cyclically fluctuating species; a rather vague paper on worm parasites; and an account of brush-cutting machinery, for clearing scrub areas, which has the real American touch of vigour and large scale operation.

The ideas contained in these papers are mostly valuable, and the only comment that occurs to one is that the actual figures and tests of hypotheses are rather limited, e.g. the game refuges were only 2000 acres in extent. But, since no excessive claims are made, the impression left is of soundness both in contribution and editing, and of considerable freshness and promise in attitude. With the vast growth of agricultural, forest, soil, water, and conservation schemes in the United States, an institution and journal of this standard will fully justify their existence if they stand by the principles that are set out in this first number.

C. E.

G. C. Grindley (1937). *The intelligence of animals.* 70 small pp. Methuen and Co., Ltd., 36 Essex Street, London, W.C. 2. Price 2*s.* 6*d.*

This book is easy to read and understand, and it will encourage the animal ecologist to wonder whether he may not after all be able to understand some of those larger books which kill the reader at the start by a barrage of technical definitions. One hopes this view

is not wrong, because many of the outstanding field problems in animal ecology (and therefore in plant ecology) hinge upon the permanence or variability of the behaviour of some animal. Will the herring always avoid the same density of diatoms during its migratory movements? Will a parasite that goes only on one host, or a beetle that attacks only one plant, continue to be conservative in another country? Will peregrine falcons nest on more than one skyscraper? How far can animals in reserves be tamed to new ways?

The author explains simply the various grades of learning power in the animal kingdom: that many invertebrates have it in small measure; that snails and worms have it but are very slow to learn anything; that the power is often overlaid in insects by extremely stiff and unyielding instincts. "The intelligence of birds, that is, the learning ability, has not been very thoroughly explored." After dealing with the mammals, the author discusses the importance of incentives to action, as indicated by various experiments. Here we would have liked to know more about the action of incentives, and what views the author has about animal consciousness.

The bibliography does not give a very adequate guide directly to the literature, for which the reader is mainly referred to N. R. F. Maier and T. C. Schneirla's *Principles of Animal Psychology*.

C. E.

Geoffrey Lapage (1937). *Nematodes parasitic in animals.* 172 small pp. Methuen and Co., Ltd., 36 Essex Street, London, W.C. 2. Price 3*s.* 6*d.*

This competent book is concerned mainly with the physiology of nematodes and with this aspect of the host-parasite relation. Parasitic nematodes make the body of an animal their chief habitat, with in some cases short journeys outside the host. The study of physiology therefore overlaps indistinguishably with what would be ecology in a free-living animal. The blood or tissues or various tubular passages have to be studied as the parasite's environment, just as we might study the microclimate of a tree-trunk for wood-boring beetles, or of soil for soil animals.

The ecologist will chiefly be interested in the results rather than in the physiological techniques. A great deal of information about the extent and nature of resistance by hosts, variation of resistence with age, host specificity, the normal physiology of nematodes, and what is known about factors stimulating development of the parasite at different stages, is packed into a small space.

The bibliography is very large, and obtrudes itself quite unnecessarily in the text owing to the spelling in capital letters of the authors' names. But for this visual obstacle, the book could be read with interest, though not with ease. It errs on the side of telling the reader too much. But the material appears to be otherwise well-arranged and the author has brought together an unusual collection of facts, not available elsewhere in this form. There is a short chapter on control of nematode pests.

C. E.

J. H. Orton (1937). *Oyster biology and oyster-culture. Being the Buckland Lectures for 1936.* 211 small pp., 57 plates and figures. Edward Arnold and Co., Ltd., 41 Maddox Street, London, W. 1. Price 5*s.*

Growing oysters is a thriving occupation in many parts of the world, and we not only grow them but import a great many from Portugal, Holland, France, and other places. The common oyster (*Ostrea edulis*) is famous in ecology because it was from the study of its associated species that Möbius first proposed the concept of the biocenosis or animal community.

This book starts with development of the young, which settle once for all at an early age, and continues with their rhythms of activity, their food (plankton, of which they eat most in late summer, getting fat for the winter), shell growth, sex changes, and spawning rhythms. They do best in estuaries and creeks, where the spat falls within nearer limits, and there is shelly sandy mud (the chief preference among many minor variants of bottom type). The temperature controls are partly known, and the demands for pure water and a fairly high salinity

Above all clear surface for the swimming larvae to settle down upon is vital, and this is supplied by good managers in the form of clean shell or tiles, etc. Other conservation measures include the removal of stock to fatten, like store cattle, on special grounds; the prevention of overfishing; and replenishment of stocks. Incidentally, the oyster owners work under long-term government leases. Very important are the enemies of the oyster, including various small whelk-like oyster-tingles (the worst (*Urosalpinx*) introduced from America), also crabs, starfish, etc. These are removed in large numbers by the fishermen. In parts of Essex and elsewhere, the slipper limpet (*Crepidula*), another American introduction, plays havoc.

There are notes on parasites, fluctuations in populations, and a fascinating glossary of the technical terms used by oyster fishermen, and a good bibliography.

C. E.

E. Ford (1937). *The Nation's sea-fish supply. Being the Buckland Lectures for 1936.* 112 small pp., 3 plates and 8 figures. Methuen and Co., Ltd., 36 Essex Street, London, W.C. 2. Price 3*s.* 6*d.*

Although the North Sea looks a fairly large fishpond, it has for some years been known for certain that man, in extending his predatory attacks upon the natural stocks of fish, has nearly reached the safe limits of exploitation. After an uninterrupted period of fishing freedom since 1866, tempered only by the periodic failure of demand, and the recommendations of the International Council for the Exploration of the Sea, the British fisheries were in 1933 placed at many points under rigid central control affecting the imports of foreign fish (in 1934 we imported six and a half million pounds of canned fish), the grounds that could be fished (those further afield being discouraged owing to the poorer quality of the fish on arrival here), the size of mesh for the trawls, and the size of the fish that could be sold.

It is this matter of the size of fish and size of mesh which depends especially upon the progress of ecological research. In fact it may be said that legislation of the kind that has been enacted could only be framed at all as the result of more than 20 years' ecological research, almost solely financed by government, and hardly at all by the British fishing industry. Another important problem in the conservation of stocks is the destruction of young fish below the marketable age, or else their use for other purposes such as manure. Here foreign shrimp fisheries play a dangerous role. Recently the matter has been considered by an international conference in London.

The author traverses in an interesting and vigorous way the various theories about under- and over-fishing. One of the special things about fish is their comparatively long life, which causes the commercial nemesis of over-exploitation to be delayed, although it can usually be detected far in advance by modern ecological methods. This makes the problem rather different from, for instance, insect pest control.

Another important feature, shared by other animal populations is the fluctuation which occurs naturally and has a serious effect of masking the influences of man. Hence the need for sustained and long term research. During the next 50 years, the human race will have to establish by scientific measures a rough equilibrium with all the animal populations that surround it, or else either one or the other will suffer, and in some places disappear. This book makes one feel, more than any that one has read, that the age of casual exploitation is nearly over.

C. E.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts, cut down to a width suitable for pasting on five-inch index cards, are issued free with the *Journal*. They can also be obtained separately by non-subscribers, from the Cambridge University Press, Fetter Lane, E.C. 4, or through a bookseller, price 3*s*. 6*d*. per annum post free (about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, J. R. Carpenter, D. H. Chitty, C. Elton, F. C. Evans, and B. M. Hobby.

1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) Marine and brackish

See also **193**

157. Brown, J. M. (1937). "Port Erin, 1936, with an Appendix by O. J. H. Davis." Rep. Rugby School Nat. Hist. Soc. for 1936: 23–33.

Mainly a full account of the seaweed zones at Port Erin, Isle of Man, and lists of species. Also notes on zonation of some animals and a long list of the marine shore fauna, and of plankton organisms taken. The Appendix deals with bird life in the southern part of the Isle.

158. Kitchin, J. A. (1935). "An introduction to the ecology of intertidal rock surfaces on the coast of Argyll." Trans. Roy. Soc. Edinb. 58: 351–74.

A study of the local distribution of common characteristic species of the intertidal zone with reference to wave action, degree and aspect of slope, and location of rock surfaces. There is found to be an upward extension of the distribution of certain littoral plants and animals in areas having a very wide splash zone, *Lamicacia* being a notable exception. *Balanus* was not found to flourish near either *Fucus* or *Ascophyllum*. Mechanical shock and splash were considered the most important factors in wave action, although these had differential effects on smooth and rough rock surfaces.

159. Alexander, W. B., Southgate, B. A. & Bassindale, R. (1935). "Survey of the River Tees. Part 2: The estuary—chemical and biological." 171 pp. Dept. Sci. Industr. Res., Water Pollution Res., Techn. Pap. No. 5: 1–171. (H.M. Stationery Office, London. Price 9*s*.)

A very important survey of the effects of pollution on a river and its estuary, containing transects of species distribution, and their relation to sewage and cyanide pollution. (Full review in J. Anim. Ecol. (1936) 5: 194–5).

160. Tetley, H. (1936). "Gulls in the Bristol District." Proc. Bristol Nat. Soc. 8: 99–103.

Local and seasonal occurrence are described. Several species breed on Steepholm in the Bristol Channel. Black-headed gulls have increased greatly in the last thirty years round Bristol, though there is no near breeding place. The commonest species on the Avon in winter are this and the herring gull.

161. Davis, H. H. (1936). "Waders in the Bristol District." Proc. Bristol Nat. Soc. 8: 106–13.

Well-arranged notes on thirty species, giving local and seasonal distribution on mud-flats, reservoirs, etc.

162. Tait, J. B. (1937). "The surface water drift in the northern and middle areas of the North Sea and in the Faroe-Shetland Channel, Part 2, Section 3." Fisheries, Scotland, Sci. Invest., 1937, No. 1: 1–60. (Edinburgh: H.M. Stationery Office. Price 3*s*.)

Drift bottles were liberated throughout the year at various stations. From those that were stranded after the shortest intervals a time-velocity curve was drawn. From this curve it was possible to calculate the distance and course travelled by drifters stranded after longer intervals. The maximum velocity was about 12¾ miles per day in April: the same time as in 1911 but earlier than in 1910. Seasonal and annual variations in this curve are occasioned by the intensity of the main motive force of the northern and middle North Sea—the Atlantic impulse. The lateness of the 1910 maximum indicates a weaker spring impulse than in the two following years. Changes in the shape and position of the various eddy systems also occur as a result of differing intensity of this pressure. For example the Great Eddy system occupied analogous positions in 1910 and 1912 with its long axis on long. 2° E., but later in 1912 slewed round to a N.W.–S.E. position as in 1911. On both occasions this was associated with a strong Atlantic incursion. This stream-current flows down the prime meridian to about 59° N. lat. where it branches into several subsidiary streams. Stream-currents appear to be of less than 30 miles in width and to flow fastest in the middle where the physical properties most resemble those of the source-waters. The properties of the stream as a whole may differ appreciably from those of the medium through or in which the current is flowing. Thus slight changes of stream direction might account for considerable salinity changes at a given position. The spreading out of a stream margin often results in closed eddy systems with the physical, chemical and biological peculiarities of the main stream. This affords an explanation of the patchy distribution of certain passive organisms.

(*b*) Freshwater

See also **168, 194, 267**

163. Keir, W. (1936). "A survey of the breeding places of the mosquitoes of Downfield District, Dundee." Trans. Perthshire Soc. Nat. Sci. 9: 148–50.

A survey in Aug. 1932 of several ponds and streams, from which mosquitoes were bred, and some notes on correlated vegetation and animal life recorded.

164. Lloyd, B. (1937). "Dragonflies at Elstree Reservoir and district." Trans. Herts. Nat. Hist. Soc. Fld. Cl. 20: 91–4.

Observations of 10 species recorded from 1934–6 on the Middlesex-Hertfordshire boundary, including a new record for Herts., *Orthetrum cancellatum*.

165. Attlee, H. G. (1937). "Dragonflies in 1935." Entomologist, 70: 13–15.

Dates of appearances of several species. Compare similar notes by the same author for 1934, ibid. 68: 278–82; for 1936, ibid. 70: 128–30.

166. Crawford, G. I. (1937). "An Amphipod, *Eucrangonyx gracilis* S. I. Smith, new to Britain." Nature, 139: 327.

Hitherto recorded only from Canada and the United States, this species was taken in 1936 from culverts below the filter beds of the Metropolitan Water Board at the Lea Bridge Waterworks. The shrimps were living in complete darkness.

167. Tattersall, W. M. (1937). "Occurrence of *Eucrangonyx gracilis*." Nature, 139: 593.

Records the presence of this species some years ago in Hackney, in the water supply of the Metropolitan Water Board.

(c) Land

168. Hine, R. L. & others (1934). "The natural history of the Hitchin region." 256 pp. Hitchin and District Regional Survey Association. Price 7*s*. 6*d*.

About three-quarters of the book deals with animals, under their taxonomic groups. Many observations on distribution, and natural history. There are also some maps of vegetation and geology, and a one-inch map of the district. (Reviewed in the J. Anim. Ecol. (1936) 5: 197–8.)

169. Bishop, J. (1937). "The nuthatch in county Durham." Vasculum, 23: 56–7.

Notes on one of Durham's rarest nesting species.

170. Boyd, A. W. (ed. by) (1936). "Reports on selected species of birds." Lancs. and Cheshire Fauna Committee, 22nd Ann. Rep....for 1935: 35–42.

Reports from a number of observers upon the distribution, numbers, and habitats of redstart, great spotted woodpecker, pochard, from Cheshire and neighbouring counties. The habitat notes are full and informative.

171. Lloyd, B. (1936). "The distribution of the grass snake in Hertfordshire, with notes on its behaviour." Trans. Herts. Nat. Hist. Soc. Fld. Cl. 20: 30–40.

Common in the south of the county, but scarce in the chalky and hilly parts of the county, and in the Chiltern Hills generally. The question of food of the grass snake is discussed: it apparently does not live much on frogs and toads in this area, though it probably takes nestling birds. There are various observations on behaviour.

172. Austin, M. D. (1937). "The insect and allied fauna of cultivated mushrooms. 3." Ent. Mon. Mag. 73: 66–7.

Two Diptera species, four Collembola, four mites, and one Myriapod, in association with mushroom manure beds.

173. Jary, S. G. & Austin, M. D. (1937). "Insects and allied pests of cultivated mushrooms." J. S.-E. Agric. Coll. Wye, No. 39: 13–14.

A fly *Leptocera heteroneura* (Sphaeroceridae) tunnelling in mushrooms. *Sciara varians* (Sciaridae) is another fly that had been found in association with mushroom manure beds.

174. Jary, S. G. & Stapley, J. H. (1936). "Investigations on the insect and allied pests of cultivated mushrooms. 6. Observations upon the Tyroglyphid mite *Histiostoma rostro-serratum*, Megnin." J. S.-E. Agric. Coll. Wye, No. 37: 67–74.

This mite lives among damp decaying vegetable debris, and is introduced on manure into mushroom beds, but does no harm to the mushrooms. It is shown to be parthogenetic, a thing scarcely known hitherto among mites.

175. Baiss, J. L. R. & Peirson, L. G. (1936). "Handlist of the Macrolepidoptera of the Marlborough District (10 miles radius)." Rep. Marlboro' Coll. Nat. Hist. Soc. for 1935, No. 84: 44–76.

A well-ordered list giving for each species the general degree of abundance, special localities, and many notes of food plants and habitats.

176. F—, L. T. (1937). "Micro-collecting. Mid-March to mid-April." Ent. Rec. 49: 32.

Useful hints for collectors. See also ibid.: 49: 50–1.

177. Fletcher, T. B. (1937). "*Evetria purdeyi*, Durrant, in Gloucestershire." Ent. Rec. 49: 33.

Reviews the known records of the distribution of this moth since first recognized in 1911 from Folkestone specimens. Its occurrence in Gloucestershire is an extension of its range in S. England.

178. St Edmundsbury & Ipswich, W. G. (1937). "Unusual larval habit of an *Ornix*." Entomologist, 70: 31.

The Tineid moth, *Ornix scoticella*, causing a mine in the leaves of *Pyrus aria* indistinguishable from that of *Lithocolletis mespilella*.

179. Tomlin, J. R. le B. (1935). "Additions to the Coleoptera of Glamorgan." Trans. Cardiff Nat. Soc. 1933, 66: 87–102.

Includes habitat notes for a number of species.

180. Donisthorpe, H. St J. K. (1937). "A preliminary list of the Coleoptera of Windsor Forest." Ent. Mon. Mag. 73: 20–8, 70–7, 110–25.

181. Kaufmann, R. R. U. (1937). "Investigations on beetles associated with carrion in Pannal Ash, near Harrogate. I." Ent. Mon. Mag. 73: 78–81.

Details of the trap used to attract the beetles are given.

182. Harrison, G. Heslop (1937). "Observations on the British Psyllidae. I." Ent. Mon. Mag. 73: 39–42.

Psylla alni, *P. försteri*, *P. bagnalli* and *P. ambigua*.

183. Johnson, C. G. (1937). "The biology of *Leptobyrsa rhododendri* Horvath (Hemiptera, Tingitidae), the *Rhododendron* lacebug. II. Feeding habits and the histology of the feeding lesions produced in *Rhododendron* leaves." Ann. Appl. Biol. 24: 342–55.

184. Harrison, G. Heslop (1937). "Observations on the biology of certain British Psyllidae." Entomologist, 70: 49–52.

Hibernation, host and shelter plants.

185. Saunt, J. W. (1932). "'Trypetidae' in Warwickshire." Proc. Coventry Nat. Hist. Sci. Soc. 1: 48–51.

Records 19 species of these Diptera, with good notes on food plants, etc.

186. Collin, J. E. (1937). "*Trypeta vectensis* sp.n. and other new or little known British species of Trypetidae (Diptera)." Ent. Rec. 49: (1)–(7).

The larvae of these flies are gall-formers, leaf-miners, or live in flower-heads or fruits.

187. Austin, M. D. (1937). "Notes on the status of flies of the family Sphaeroceridae (Borboridae) in the economy of cultivated mushrooms." Proc. R. Ent. Soc. Lond. A, 12: 15–16.

Larvae introduced with the manure composts used for mushroom beds may be potential pests.

188. Goffe, E. R. (1937). "*Sziladynus luridus* Fall. (Dipt., Tabanidae) taken in England and a further English locality for *Sziladynus montanus* Meig." J. Soc. Brit. Ent. 1: 189.

Both of these flies are not uncommon in the Scottish Highlands, but the first has not hitherto been recorded in England.

189. Wilson, G. Fox (1937). "Mole crickets a garden pest in Hants." Ent. Rec. 49: 85–6.

At Mudeford, Christchurch, 12 acres, chiefly kitchen garden, were infested. In one part, about 70 sq. yds. which had not been dug for two years, 82 were taken—all in the wettest part, where some of the ground had been under water during the winter.

190. Freeman, P. (1937). "New British localities for *Metrioptera roeselii*, Hagenbach, and *Metrioptera brachyptera*, L. (Orthoptera, Tettigoniidae)." Ent. Rec. 49: 34–5.

The first of these two grasshoppers, hitherto considered a littoral species in Britain, is now recorded some distance inland in Essex.

191. Abbott, M. J. (1936). "The Rugby humble-bees." Rep. Rugby School Nat. Hist. Soc. for 1935: 26–31.

Records 12 species of *Bombus*, and six of *Psithyrus*, with some notes on abundance, distribution and flowers frequented.

192. Harrison, J. W. Heslop (1937). "The gallmaking sawflies of the genus *Pontania* in Durham and Northumberland." Entomologist, 70: 73–5.

Notes on *P. viminalis*, *P. pustulator*, *P. vesicator*, *P. phylicifoliae*, *P. robbinsi*, *P. proxima* and *P. pedunculi*.

(*d*) Small islands

See also **227, 258**

193. Goddard, T. Russell (1937). "A guide to the Farne Islands." 32 pp. (Andrew Reid and Co., Strawberry House, Newcastle upon Tyne. Price 6*d*.)

A most useful small guide to the history and the bird and seal populations of this sanctuary. Four bird watchers are maintained during spring and summer to afford this one-time hunting ground the protection it must so obviously continue to enjoy. Their duties include the attempted control of predatory gulls (lesser black-backed and herring) by means of the collection of their eggs. Besides notes on the sea-birds, which form the main section, there is some information about grey seals and wild rabbits. There is a good map showing the high water and low water zones on the islands.

194. Forrest, J. E., Waterston, A. R. & Watson, E. V. (1936). "The natural history of Barra, Outer Hebrides. The results of a scientific expedition organised by the Biological Society of the University of Edinburgh, 1st–14th July 1935." Proc. R. Phys. Soc. Edinb. 22: 241–96.

Lists of plants and animals of various groups, but not arranged in communities. Some useful distribution data, and ecological notes on many species. *Gammarus duebeni* was the shrimp found in fresh water streams. The estuarine shrimp *Neomysis vulgaris* occurred in an almost fresh loch. (Reviewed in J. Anim. Ecol. (1937) 6: 203, and in J. Ecol. (1937) 25: 265–6.)

195. Harrison, G. H. (1937). "A contribution to our knowledge of the Lepidoptera of the islands of Eigg, Canna, and Sanday." Ent. Rec. 49: 29–31.

An interesting list of butterflies and moths with notes on their habitats and abundance.

196. Jeffery, H. G. (1936). "Coleoptera. A fourth supplementary list of the Coleoptera of the Isle of Wight...." Proc. Isle of Wight Nat. Hist. Soc. for 1935: 483–93.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

See also Section 4, for parasites

197. Sandars, E. (1937). "A beast book for the pocket: the vertebrates of Britain, wild and domestic, other than birds and fishes." 378 pp. (Oxford University Press. Price 7*s.* 6*d.*)

An excellent guide to the species, illustrated in colour and black and white, with sketch maps showing distribution. (Reviewed in J. Anim. Ecol. (1937) 6: 202.)

198. Chard, J. S. R. (1936). "British animal tracks." 80 pp. (C. Arthur Pearson, Ltd., London. Price 3*s.* 6*d.*)

Gives descriptions and figures of tracks of 32 species of wild mammals, and how to distinguish them from domestic animals. (Reviewed in J. Anim. Ecol. (1937) 6: 201.)

199. Chrystal, R. N. (1937). "Insects of the British woodlands." 338 pp. Frederick Warne and Co. 1–4 Bedford Court, Strand, London, W.C. 2. Price 7*s.* 6*d.*

A well-arranged guide to those insects that are actual or potential pests on forest trees in Britain, with very good drawings, photographs and keys to classification. A few other insects of woodland are also described, mostly beetles. There is no general list of woodland insects or of communities. (Reviewed in J. Anim. Ecol. (1937) 6: 372–3.)

200. Royal Entomological Society of London, Committee on Generic Nomenclature (1937). "The Generic Names of British Insects. Part 4. The generic names of the British Neuroptera, with a check list of the British species," by **F. J. Killington.**

These lists, based upon a careful examination of the literature, should do much to standardize the nomenclature of British insects. Previous parts deal with general recommendations, butterflies and dragonflies.

201. Killington, F. J. (1937). "A monograph of the British Neuroptera." Ray Society, London, 2: 1–306. Price 25*s.*

A complete account of the present state of knowledge of the British Neuroptera (*sensu stricto*, lacewings) written for both the biologist and the systematist.

This second and final volume concludes the discussion of the Hemerobiidea, embraces the whole of the Chrysopidae, the genera *Boriomyia* and *Kimminsia*, and gives appendices on collecting, preserving and rearing, a bibliography, and index.

202. Richards, O. W. (1937). "A study of the British species of *Epeolus* Latr. and their races, with a key to the species of *Colletes* (Hymen., Apidae)." Trans. Soc. Brit. Ent. 4: 89–130.

Gives key to the species of host-bees (*Colletes*), discusses their size, flight period, distribution and habits. Considers the nomenclature of the parasitic bees (*Epeolus*), their identification, distribution, host attributions, relations to host, variation and racial differences.

203. Nixon, G. E. J. (1937). "The British species of *Dacnusa* (Hym., fam. Braconidae)." Trans. Soc. Brit. Ent. 4: 1–88.

Keys and descriptions of all the known British species of this difficult genus of parasitic Hymenoptera illustrated with 22 plates. 68 spp. occur in Britain, 31 of which are here described as new.

204. Jones, H. P. (1937). "A new British 'mason wasp'." Ent. Mon. Mag. 73: 13–15.

Microdynerus exilis in Hampshire.

205. Fisher, R. C. (1937). "The genus *Scolytus* in Great Britain, with notes on the structure of *S. destructor* Ol." Ann. Appl. Biol. 24: 110–30.

Contains a key to species found in Great Britain with notes on habitat.

206. Burr, M. (1936). "British grasshoppers and their allies: a stimulus to their study. 162 pp. (Philip Allan and Co., 69 Great Russell St, London, W.C. 1. Price 6*s*.)

Small text-book to species and their distribution. (Reviewed in J. Anim. Ecol. (1937) 6: 200–1.)

207. Gaskin, L. J. P. (1937). "On a collection of original sketches and drawings of British sea-anemones and corals by Philip Henry Gosse, and his correspondents, 1839–61, in the library of the Horniman Museum." J. Soc. Bibl. Nat. Hist. 1: 65–7.

This collection comprises about 200 items in pencil and colour with many notes on localities, dates and observations on behaviour.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **158, 159, 171, 245, 261**

208. Collenette, C. L. (1937). "Bracken in Richmond Park." London Nat. for 1936: 44–5.

Bracken is probably deteriorating in the Park. It has certain important ecological effects, e.g. dead bracken affords nest cover for stonechat, whinchat, woodlark, tree and meadow pipits, yellow and reed buntings, and pheasant. The only other ground cover that, like bracken, is not grazed down by the deer, is rushes. Without bracken, the birds mentioned, except the last, would probably disappear. Bracken hinders establishment of birch and *Rhododendron* seedlings. The latter grow up round badger earths, where the ground cover has been opened up. In such a park, bracken also has an important aesthetic value, and is not there a pest. Deer strongly influence the vegetation, and prevent tree regeneration. Commons fenced from deer have scrub.

209. Watt, A. S. (1937). "Studies in the ecology of Breckland. 2. On the origin and development of blow-outs." J. Ecol. 25: 91–112.

On p. 109 there is a discussion of rabbit influence upon the formation of blow-outs on this inland sand area. It is shown that rabbits are not important agents, although they are said to be on coastal dunes in Norfolk.

210. Temperley, G. W. (1937). "Grebes, smews and little auks." Vasculum, 23: 76.

After strong N.E. gales, various grebes and few smews appeared on local inland waters. Many little auks were blown inland and were picked up dead.

211. Armishaw, J., Edwards, J. H., Shotton, F. W. & Wright, J. (1933). "Gregarious hibernation of smooth newts." Proc. Coventry Nat. Hist. Sci. Soc. 1: 74.

30 smooth newts, apparently less than a year old, hibernating in small cavity in stiff clay, below surface in cracked ground. Nearest water 40 yd.

212. Van Someren, V. D. (1937). "A preliminary investigation into the causes of scale absorption in salmon (*Salmo salar*, Linné)." Fisheries, Scotland, Salmon Fish., 1937, No. 2: 1–12. (Edinburgh: H.M. Stationery Office. Price 9*d*.)

Serum calcium values of 27 male salmon were fairly constant at 15·5 to 16·0 mg. % until just before spawning when the value fell to 11·1 mg. %. In 23 females the value rose during the period of upstream migration from 18–19 mg. % to 44·2 mg. % then fell to 11·8 mg. % just before spawning. These variations were independent of weight, length, condition, or the degree of scale absorption. Scale absorption is greater in males possibly due to the greater demand for calcium of the secondary sexual characters.

213. Cooper, L. H. N. (1935). "Iron in the sea and in marine plankton." Proc. Roy. Soc. B, 118: 419–38.

Study of iron content of the sea and of phyto- and zooplankton in English Channel, using two very sensitive colour indicators recently developed. The amount in solution is very small, and fairly large amounts are present in the animals and plants at any time. The factors controlling the availability of iron are analysed, and there is a diagram of the iron-cycle in the sea. This subject has an important bearing because it is probable that the richer plankton found in coastal waters is due to the larger amount of iron coming from the land. Diatoms require more iron than phosphorus.

214. Margary, I. D. (1937). "Report on the phenological observations in the British Isles from December, 1935, to November, 1936." Quart. J. R. Meteorol. Soc. 63: 219–75.

This report includes as usual scattered notes upon the occurrence and migration of birds, insects and some other animals, but is mainly concerned with the correlation between plant seasonal events and weather. It is announced that the system of observation is to be reorganized, and will include some standardized observations on dates of insect appearance by H. C. Gunton, who will in future supervise the reports.

215. Harding, W. J. (1937). "*Vanessa cardui* and *V. atalanta* at Lyme Regis in Winter." Entomologist, 70: 105.

Single specimens of *V. atalanta* basking in the sun between November and April.

216. Dannreuther, T. (1937). "*Vanessa atalanta* active indoors in January." Entomologist, 70: 63.

217. Fox-Wilson, G. (1937). "Insects captured in the flowers of *Nymphaea capensis* Thunb." Proc. R. Ent. Soc. Lond. A, 12: 31–9.

Observations on water lilies in a heated tank have shown that a number of pollinating insects (Hymenoptera and Diptera) are killed in the flowers. Death is apparently due, in some cases, to a fermenting alcoholic liquid in the stigmatic basin.

218. Varley, G. C. (1937). "Aquatic insect larvae which obtain oxygen from the roots of plants." Proc. R. Ent. Soc. Lond. A, 12: 55–60.

This habit and the correlated structural modifications of the spiracles have originated independently in two families of Coleoptera and three families of Diptera.

219. Britten, H. (1937). "*Taeniorrhynchus richardii* Fic. and *Culex pipiens* L. feeding on the flower heads of creeping thistle (*Cnicus arvensis* Curt.)." North Western Nat. 12: 57.

Mosquitoes swarming on thistle flowers.

220. Oldham, C. (1936). "Note on the fairy shrimp (*Chirocephalus diaphanus*)." Trans. Herts. Nat. Hist. Soc. Fld. Cl. 20: 24.

Survived one year's, and in another pond, two years' drought.

221. Lambert, F. J. (1936). "Jellyfish. The difficulties of the study of their life history and other problems." Essex Nat. 25: 70–86.

Notes on some of the methods used in studying the development and feeding habits of jellyfish on the Essex coast, belonging to the genera *Aurelia*, *Chrysaora*, *Cyanea*, and *Rhizostoma*. *Aurelia* was kept in an aquarium for five years. Other observations were done at pools on the mud flats during the winter months. (An extra note by same author, ibid. p. 170.)

222. Atkins, W. R. G. & Poole, H. H. (1936). "Photoelectric measurements of the luminous efficiency of daylight." Proc. Roy. Soc. B, 121: 1–17.

Tests carried out with the Weston selenium rectifier cell.

223. Atkins, W. R. G., Poole, H. H. & Stanbury, F. A. (1937). "The measurement of the intensity and the colour of the light in woods by means of emission and rectifier photoelectric cells." Proc. Roy. Soc. B, 121: 427–50.

4. PARASITES

See also, **202, 203**

224. Britten, H. (1936). "Insects and Acari. Additions and corrections to the Lancashire and Cheshire lists for 1935." Lancs. and Cheshire Fauna Committee, 22nd Ann. Rep. for 1935: 44–9.

Besides distribution notes on many other groups, there are records of Mallophaga from birds, a louse from the grey squirrel, and a flea from the pigmy shrew.

225. Thompson, G. B. (1937). "The parasites of British birds and mammals. XI. Records of *Ornithomyia* spp. (Diptera, Hippoboscidae) from British birds." Ent. Mon. Mag. 73: 47–51.

O. avicularia appears to come almost entirely on owls, hawks, and pigeons; *O. fringillaria* mainly on waders, game-birds, and passerines. These flies practically never come on true water birds.

226. Saunt, J. W. (1933). "Some unusual insects from the nesting boxes in the Nature Reserve." Proc. Coventry Nat. Hist. Sci. Soc. 1: 72–3.

Three cases of unfinished bumble bee nests. Pupae of parasitic fly *Ornithomyia avicularia* in box used by green woodpecker.

227. Thompson, G. B. (1937). "The parasites of British birds and mammals. XII. On some parasites from the burrows of puffins." Ent. Mon. Mag. 73: 87–8.

A collection from Sheep Island, North Antrim, Northern Ireland, contained one species of tick, one mite, and one flea.

228. Thompson, G. B. (1937). "The parasites of British birds and mammals. XIII. Records of Siphonaptera bred from birds' nests." Ent. Mon. Mag. 73: 105–7.

A useful list of records. Birds seldom carry fleas, which live chiefly in the nests.

229. Thompson, G. B. (1937). "The parasites of British birds and mammals. XIV. Records of Mallophaga from birds." Ent. Mon. Mag. 73: 134–6.

230. Thompson, G. B. (1937). "The parasites of British birds and mammals. XV. Bird-fleas and their hosts." Ent. Mon. Mag. 73: 137–42.

A full table giving the British bird hosts of 13 species of fleas, compiled from published notes and from some collections.

231. Hockley, A. R. (1937). "Progress Report No. 13. An investigation of Holostomiasis in Avon coarse fish." Rep. Avon. Biol. Res. 1935–6. No. 4: 103–6.

Infection of larvae of trematode parasite, *Neodiplostomum*, in chub, roach, dace, and minnows in the Avon; and in white bream in Great Ouse. Experiments in transmitting the worm to its final stage in water birds were not successful.

232. Ullyett, G. C. (1936). "Host selection by *Microplectron fuscipennis*, Zett. (Chalcididae, Hymenoptera)." Proc. Roy. Soc. B, 120: 253–91.

An important review of the whole problem of host selection by insect parasites, and the degree to which selection is random, and the means by which parasites recognize differences in between various hosts and between hosts in different states, e.g. whether previously parasitized or not.

233. Donisthorpe, H. (1937). "*Euplecti* as Myrmecophiles." Ent. Rec. 49: 4–5.

These Pselaphid beetles have hitherto been considered only accidental ant guests, but as so many of them are frequently found in company with ants, and occasionally in large numbers, it would appear better to consider them definite myrmecophiles.

234. Hobby, B. M. (1937). "Parasitic Hymenoptera bred from British Lepidoptera-Heterocera by H. C. Hayward, M.A., F.R.E.S." J. Soc. Brit. Ent. 1: 184–5.

Records 14 spp. of parasites with their hosts.

235. Carpenter, G. D. H. (1937). "A note on some parasites of *Zygaena* (Lep.)." J. Soc. Brit. Ent. 1: 176–8.

Out of a total of 954 burnet moth cocoons examined, 617 apparently produced imagines, and 76 apparently contained healthy living pupae: 261 failed to produce imagines.

236. Poulton, E. B. (1937). "Emergence of the parasitic Ichneumonid *Orthopelma luteator* Grav. from the gall of *Rhodites rosae* (L.)." J. Soc. Brit. Ent. 1: 179.

This parasite is frequently bred in greater numbers than the *Rhodites*.

237. Blair, K. G. (1937). "Parasites of *Epicypta testata* Edw. (Myceto-philidae)." Ent. Mon. Mag. 73: 19.

A Bethylid, *Xenotoma* (*Zelotypa*) *fallax*, and an Ichneumonid, *Aperileptus* sp.

238. Carleton, M. (1937). "A new Ichneumonid (*Scopimenus pygobarbus*) parasitic on *Nematus proximus* Lep. (Hym., Tenthredinidae) in Britain. With a description of the adult fly by Dr A. Roman." Ent. Mon. Mag. 73: 61–5.

Contains figures of comparative abundance. Out of 5136 sawfly cocoons, the following imagines emerged: 1394 *N. proximus*, 153 *Angitia vestigialis* and 3 *S. pygobarbus*. Nine parasites (out of about 20 on record) were bred at Long Ashton, Bristol.

239. Britton, E. B. (1936). "A record of the parasitic mite—*Pediculoides ventricosus* (Newp.) in Monmouthshire." Trans. Cardiff Nat. Soc. 1934, 67: 109–10.

Parasitizing larvae of elm bark beetle (*Scolytus destructor*). Only once before found indigenous in this country, although it is introduced on timber occasionally. It can cause dermatitis in man.

240. Beck, R. (1937). "*Mermis* thread worm (Nematode) in wasp (*Vespa vulgaris*)." Ent. Rec. 49: 65.

Extensive parasitization of a colony of wasps by nematode worms. Infected workers were very large and resembled queens.

5. FOOD AND FOOD-HABITS

See also **171, 191, 208, 209**

241. Oldham, C. (1936). "Food of the grey squirrel (*Sciurus carolinensis*)." Trans. Herts. Nat. Hist. Soc. and Fld. Cl. 20: 86–7.

Spruce seeds, sycamore "keys", yew fruit. These are new food records. The method of gnawing the spruce cones is described.

242. Berry, J. (1936). "British mammals and birds as enemies of the Atlantic salmon (*Salmo salar*)." Rep. Avon Biol. Res. 1934–5, No. 3: 31–64.

Only about 2% of smolts leaving a river eventually get caught as adults. The chief mammal enemies are thought to be for the larger fish, seals, porpoises, otters, and for the smaller fish and spawn, water shrews (and to some extent rats, but not water voles). The fish-eating habits of a number of birds are discussed. The evidence both for birds and mammals is based mainly on casual observations, or else on "general experience", and full studies appear to be badly needed. There are also complications, as that the otter eats many eels and pike, which themselves are enemies of salmon. There is a full bibliography.

243. Craster, J. M. (1937). "Fulmar petrels on the Northumbrian coast." Vasculum, 23: 36.

Notes on feeding behaviour.

244. Moon, H. P. (1937). "Progress Report No. 10. The food of the smolt of *Salmo salar* in the River Avon (Hampshire)." Rep. Avon Biol. Res. 1935–6, No. 4: 85–88.

In spring 1936 smolts were trapped and marked during their migration to the sea. 85 that were accidentally killed were used for food investigation. A complete list of the food animals is given, with percentage occurrence, and total numbers eaten. Most of the food was Chironomid fly larvae, caddis larvae, and insects taken at the surface. They had been feeding mainly on stony areas with a fast current. The results suggest that Mollusca were avoided.

245. Hooper, C. H. (1936). "Plums: Notes on their pollination, order of flowering of varieties and insect visitors to the blossoms." J. S.-E. Agric. Col. Wye, No. 37: 131–40.

The flowering periods of different varieties of plum differ greatly, over a period of about 30 days. Brief notes are given on some of the insect visitors, and the importance of bees emphasized. "If insects are excluded from plum blossoms very few fruits mature."

246. Parmenter, L. (1937). "Predacious flies and their prey." London Nat. for 1936: 51–4.

Gives 31 examples of the prey of nine species, with good details of species, sex, locality, habitat, date, and some observations on habits.

247. Jones, F. M. (1937). "Relative acceptability and poisonous food-plants." Proc. R. Ent. Soc. Lond. A, 12: 74–6.

Previous papers by this author have shown that some brightly coloured insects are relatively unacceptable to certain birds and that extracts of these same insects when mixed with foods otherwise acceptable to ants prevent or deter the ants from consuming these foods. The present paper shows that infusions of freshly-fed and starved insects are both avoided by ants proving that the insects retain their deterrent qualities whether they have recently fed on poisonous plant material or not.

248. Marshall, J. F. & Staley, J. (1937). "Some notes regarding the morphological and biological differentiation of *Culex pipiens* Linnaeus and *Culex molestus* Forskål (Diptera, Culicidae)." Proc. R. Ent. Soc. Lond. A, 12: 17–26.

Two distinct species of mosquito—one a man-biter and the other a man-ignorer—have been confused under the name *Culex pipiens*. The name *C. molestus* should be revived for the first and *C. pipiens* reserved for the second. At least 7 varieties of *C. molestus* are known.

249. Pearce, E. J. (1937). "Notes on the feeding-habits, etc., of some of the British Haliplidae." Ent. Mon. Mag. 73: 1–6.

These water-beetles are chiefly vegetarians, but will eat dead flies.

250. Prideaux, R. M. (1937). "Food-plant of *Tyria jacobaeae*." Entomologist, 70: 20.

The larvae will feed on the blooms of *Senecio Greyi*.

251. Wakely, S. (1937). "Food-plant of *Tyria jacobaeae* Linn." Entomologist, 70: 70.

Senecio erucifolius in addition to the common food plants *S. jacobaea* and *S. vulgaris*.

252. Milman, P. P. (1937). "*Porthesia similis*: larval food-plants." Entomologist, 70: 69–70.

Leaves of pear, apple, gladioli, *Lilium auratum*, and fruit of loganberry and apple.

253. Blair, K. G. (1937). "Midges attacking Meloë beetles." Ent. Mon. Mag. 73: 143.

254. Wimpenny, R. S. (1937). "The distribution, breeding and feeding of some important plankton organisms of the south-west North Sea in 1934. Part 1. *Calanus finmarchicus* (Gunn), *Sagitta setosa* (J. Müller) and *Sagitta elegans* (Verrill)." Ministry Agr. Fish., Fish. Invest. (1936), Ser. 2, 15, No. 3: 1–53. (London: H.M. Stationery Office. Price 3*s*.)

The May–July diatom growth was responsible for successful brood survivals in all 3 species. Egg patches of *Calanus* and *S. setosa*, in contrast to the species as a whole, were generally in or near diatom patches which probably act as breeding or nursery grounds. The largest individuals were those born at the coldest time of year. The size of all species was less than that found in deeper water by another worker and *S. setosa* decreased in size from north to shallower south. The proportion of feeding *Calanus* fell with age from 91% (stage I) to 54% (stage V) after which 49% males and 75% females were feeding. In October all three species were feeding most heavily in the diatom-rich south, but this may have been inversely related to population density.

255. Cole, H. A. (1937). "Experiments in the breeding of oysters (*Ostrea edulis*) in tanks, with special reference to the food of the larva and spat." Ministry Agr. Fish., Fish Invest. (1936), Ser. 2, 15, No. 4: 1–25. (London: H.M. Stationery Office. Price 2*s*.)

It had been previously found that physical conditions were not the main factors limiting successful tank breeding. 1936 experiments were therefore concerned with food requirements. Two 90,000 gallon tanks were each given a breeding stock of 400 new oysters, plus 100 remaining from the previous year. During July a population of 100,000 spat had settled on tiles set as collectors on the bottom of the control tank A (sea water only). In tank B (sea water enriched with finely ground crab) every clean surface was so densely covered with spat the numbers could not be estimated. In tank B the density of all nannoplankton was considerably the greater; in both tanks growth and settlement of larvae were associated with presence of minute naked flagellates. These organisms appear to be the sole food utilisable during 8–11 days of larval life. Settled spat, however, will thrive on green unicells such as *Coccomyxa littoralis* (impure culture), possibly because the firm cell walls can be penetrated in the course of a passage through the gut that is considerably less rapid than in the larvae. A proportion of larvae were inherently non-viable and may have been produced by oysters that had deteriorated under enclosed conditions.

6. ANIMAL POPULATIONS

See also **160, 170, 193, 210, 254, 255, 285**

256. Gent, C. J. (1937). "A note on the present status of the red squirrel (*Sciurus vulgaris*) in Northumberland." Vasculum, 23: 55–6.

In many districts the red squirrel is again increasing in numbers.

257. Perry, R. K. (1936). "A summary of the grey squirrel (*Sciurus carolinensis* Gmelin) in Cheshire." Lancs. and Cheshire Fauna Committee, 22nd Ann. Rep. for 1935: 11–15.

Gives a large table of records for various years and places.

258. Wadham, P. (1937). "Notes on the fishes, reptiles, and mammals of the Isle of Wight." Proc. Isle of Wight Nat. Hist. Soc. for 1936: 598–601.

Occurrence of seven species of marine fish. Green lizard (*Lacerta viridis*) introduced in 1899 still breeds here. Foxes are numerous in spite of persecution, living among the cliffs. The harvest mouse (*Mus minutus*) is very scarce, owing probably to changes in the hedges on the island. The yellow-necked field mouse (*Apodemus flavicollis wintoni*) is recorded for the first time. House mice have decreased, also rats. Rabbits are at present very abundant: the causes of this are discussed.

259. Fitter, R. S. R. (1937). "The starling roosts of N.E. Surrey." London Nat. for 1936: 72–5.

Notes on roosts and feeding areas, not summarized or mapped.

260. Ticehurst, N. F. (1936). "The mute swan in Hertfordshire." Trans. Herts. Nat. Hist. Soc. Fld. Cl. 20: 74–84.

An interesting summary of the history of swan keeping, referring especially to this county (Rivers Colne and Lee). The protection of swans dates back to at least 1230, and is one of the oldest instances of deliberate game management in England.

261. Boyd, A. W. (1936). "Great-crested grebe in Cheshire." Lancs. and Cheshire Fauna Committee, 22nd Ann. Rep. for 1935: 33–4.

In 1931 there were 80 breeding pairs, and in 1935 there were 77–84. The drought in 1933 and 1934 caused local changes, but the county as a whole had very similar populations in these two years of census. Details are given.

262. Glegg, W. E. (1935). "The history of Essex heronries: additional colonies." Essex Nat. 25: 51–2.

Two additional sites, one extinct and one occupied, making total known of 21 extinct and 10 occupied.

263. Boyd, A. W. (1936). "Status of the woodcock in Cheshire." Lancs. and Cheshire Fauna Committee, 22nd Ann. Rep. for 1935: 27–32.

Gives detailed tables of records, whether breeding, time of occurrence, abundance, and in some cases breeding habitat and shooting bag records.

264. Menzies, W. J. M. (1936). "Sea trout and trout." 230 pp. Edward Arnold and Co., 41 Maddox St, London. Price 10*s.* 6*d.*

A general account of scientific and practical work on these fish, with special reference to Scottish waters. (Reviewed in J. Anim. Ecol. (1936) 5: 400.)

265. Wood, H. (1936). "Race investigation of the herring population of Scottish waters." Fisheries, Scotland, Sci. Invest. 1936, No. 3: 1–52. (Edinburgh: H.M. Stationery Office. Price 2*s.* 6*d.*)

Herring in Scottish waters belong to two distinct physiological groups: spring and autumn spawners. The spawning grounds of the former (sea temp. lowest, 5·13–7·33° C.) are under Atlantic influences with the exception of one area at the mouth of the Forth estuary. The autumn spawners (sea temp. highest, 10·93–12·60° C.) live entirely within the North Sea. Counts of vertebrae and keeled scales between vent and pelvic fin reveal mean Vert. S and mean K_2 are respectively higher and lower in spring spawners (but the Forth estuary community is very variable). The autumn spawners show an increase in mean K_2 from North to South, and this tendency is maintained in the middle and south North Sea spawners. While the various groups remain separate in the adolescent stage, adults from at least 3 stocks combine in proportions varying with time and place to compose the summer and autumn fishing stocks.

266. Anon. (1935). "Saorstát Éireann [Irish Free State] Report on the sea and inland fisheries for the year 1935." Pp. 1–32. (Government Publications Sale Office, 5 Nassau St, Dublin, C. 2. Price 9*d.*)

The quantity and value of the Irish Free State sea fishery have fallen steadily from 1927 (£450,000) to 1934 (£160,000). The 1935 landings showed a slight rise in quantity on 1934 but a drop in value largely because nearly 30% of the deep sea catch was whiting of small size and value. Imported fish were valued at £264,953, those exported at £270,224. The hatchery output of salmon and trout fry for inland fisheries was almost 7 million. Some 6600 persons are engaged part-time in inland fishery operations.

267. Moon, H. P. (1937). "Progress Report No. 1. Ecology. Importance of environment on aquatic life." Rep. Avon Biol. Res. 1935–6, No. 4: 24–8.

Outlines a scheme for studying the bottom fauna in relation to silt, and to availability of different animals for fish food. For this purpose an apparatus for sorting out the animals from the silt collected for quantitative work, is described.

268. Thompson, H. W. (1935). "Plant pests in Glamorgan. 3." Trans. Cardiff Nat. Soc. 1933, 66: 103–9.

List of a large number of insects, some mites and nematodes, and two slugs, and the species damaged by them.

269. Fryer, J. C. F. (1936). "*Hyponomeuta rorellus* in Suffolk and Norfolk (Lep.)." Entomologist, 69: 269–70.

Notes on a severe outbreak of this moth on *Salix alba*. The only parasite so far bred from this species is *Herpestomus brunnicornis*. Further information in **E. T. Goldsmith**, ibid.: 217–18; **J. C. F. Fryer**, 1937, ibid. 70: 91–2.

270. F[ryer], J. C. F. (1937). "Recent caterpillar plagues in Great Britain." Nature, 140: 94–5.

(1) Outbreak of antler moth caterpillars (*Charaeas graminis*) on hill pastures in the north of England and in Scotland. The larvae eat *Festuca*, *Nardus* and similar grasses on poorer pasture. They occasionally (as in 1937 and earlier years mentioned) devastate the grassland and migrate in swarms. There have been previous outbreaks also in Wales. They do not usually last more than one year. Their cause is unknown. (2) Outbreak of the willow small ermine moth (*Hyponomeuta rorella*) on *Salix alba* (but apparently not on cricket-bat willow or sallow) in Suffolk in 1937. It is not a permanent resident in England, but was noted in Suffolk and Norfolk in 1936. It is possible that the increase was due to arrivals without their normal parasites, and this idea was supported by the very low rate of parasitism found. The damage and the web-forming habits make the attack rather spectacular. (See photos: *Illustrated London News*, 10 July, 1937, p. 66.)

271. Fraser, F. C. (1937). "*Sphinx pinastri* L. (Lep.) in Bournemouth." J. Soc. Brit. Ent. 1: 191–2.

This hawk-moth, hitherto considered a great rarity, has in recent years become abundant in the neighbourhood of Bournemouth.

272. Barnes, H. F. (1937). "Methods of investigating the bionomics of the common crane-fly, *Tipula paludosa* Meigen, together with some results." Ann. Appl. Biol. 24: 356–68.

Longevity of adults in captivity, time of day of emergence and egg laying, number of eggs laid and duration of this stage. Description of Petri dish method of rearing larvae to third instar.

273. Donisthorpe, H. (1937). "*Polygraphus polygraphus*, L., in Suffolk and Norfolk." Ent. Rec. 49: 33–4.

Except for a single record in 1925, this bark-beetle had not been taken in Britain for nearly 70 years. In 1936 it was found in great numbers killing spruce in Suffolk.

274. Gimingham, C. T. (1937). "Hover flies killed by a fungus." Trans. Herts. Nat. Hist. Soc. Fld. Cl. 20: 155–6.

Wholesale destruction of a Syrphid, *Melanostoma* sp., by *Empusa muscae* in Bedfordshire, August, 1936. Several days of normal activity elapse between infection and death.

275. Needham, N. V. (1937). "A bacterial disease of *Aphis rumicis* Linn., apparently caused by *Bacillus lathyri* Manns and Taubenhaus." Ann. Appl. Biol. 24: 144–7.

276. Buxton, P. A. (1937). "The numbers of males and females in natural populations of head-lice (*Pediculus*: Anoplura)." Proc. R. Ent. Soc. Lond. A, 12: 12–4.

The ratio of males to females increases as the head becomes more densely infested. Experiments suggest that this is due to the unfavourable effects of frequent pairings upon the females, so that they die sooner than they would otherwise and so become rarer in the population. An interesting analogy is drawn with the relation of predators to a population of prey, e.g. *Paramecium* and yeast cells.

277. Matheson, C. (1935). "The oyster fishery at Mumbles, Glamorgan." Trans. Cardiff Nat. Soc. 1933, 66: 81–6.

An account of the historical importance and later decline of the oyster fisheries on the south coast of Glamorgan, in the Bristol Channel. Measures are being taken to try and revive the fishery, whose decline was partly due to over-fishing and partly to natural causes.

278. McCloy, J., Dodd, J. M., Davies, H. C., Edmonds, F. B. J. & Orton, J. H. (1937). "Rate of growth of totally submerged *Cardium edule*." Nature, 139: 799–800.

Data from New Brighton for 1933–6 indicate that the customary marked decrease in length of this bivalve at later ages is not apparent within this period. Unfavourable conditions doubtless account for the relatively poor growth rate observed among the cockles.

279. Taylor, C. B. (1936). "Short-period fluctuations in the numbers of bacterial cells in soil." Proc. Roy. Soc. B, 119: 269–95.

Two-hourly sampling of soil at Rothamsted gave significant fluctuations in the bacterial populations. These could not be correlated with each other or with any known external factor, and it is concluded that soil bacteria undergo irregular fluctuations due to their own interrelations. This idea is supported by inability to maintain constant bacterial populations even when the medium is kept quite uniform.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **162, 210, 258, 264, 265, 270**

280. Thomson, A. Landsborough (1936). "Bird migration." 224 pp. (H. F. and G. Witherby Ltd., 326 High Holborn, London, W.C. 1. Price 5*s*.)

General introduction to the subject. (Reviewed in J. Anim. Ecol. (1937) 6: 202.)

281. Blackburne, C. I. (1937). "An experiment in migration with young white storks." Proc. Isle of Wight Nat. Hist. Soc. for 1936: 595–7.

In June 1936 the Haslemere Educational Museum imported 23 storks from East Prussia. 19 were kept in North Kent and four in Scotland. The birds were about five weeks old on arrival. They were released on Aug. 12th. After various wanderings on the south coast, during which they were mainly unmolested owing to the publicity given to the experiment, they disappeared and are assumed to have flown to Africa. The experiment proved that the young would leave the country without parental guidance.

282. T[emperley], G. W. (1937). "A waxwing winter." Vasculum, 23: 75–6.

Waxwings have almost become annual visitors; this season they were more than usually plentiful and widely distributed in the North of England.

283. Glegg, W. E. (1936). "Essex bird-migration." Essex Nat. 25: 123–157; **(1937)**, 25: 192–207.

General summary of facts known about migration in Essex, including lighthouse observations and ringing.

284. Temperley, G. W. (1937). "Ornithological report for Northumberland and Durham for the year 1936." Vasculum, 23: 45–7.

Summer migrants were later than in the previous year. Winter visitors were fairly numerous.

285. Hartley, G. W. (1937). "Salmon caught in the sea—north-west Sutherland, 1936." Fisheries, Scotland, Salmon Fish., 1937, No. 3: 1–21. (Edinburgh: H.M. Stationery Office. Price 1*s*.)

Grilse formed over 80% of the catch, the biggest run being in the first 10 days of July. Smolt ages were high as might be expected from the high latitude (2 year: 68·7%; 3 year: 29·1%). The presence of one- and four-year smolt ages (0·7 and 1·5%) indicates a mixed stock from the south and north. This heterogeneity is further demonstrated by means of a useful application of Holmes' mathematical method of sand sample analysis. Growth increment is greatest in July.

286. Hardy, A. C. & Milne, P. S. (1937). "Insect drift over the North Sea." Nature, 139: 510–1.

730 specimens, chiefly small Diptera and Aphididae, were taken by net collections made at sea, in some cases 120–50 miles from the English coast. "A large population of 'aerial plankton' drifting across the sea" is indicated. Some areas were markedly richer than others.

287. Brett, G. A. (1937). Ent. Rec. 49: 18.

During 1936, 47 red admiral butterflies were marked on both hindwings with green cellulose paint in Surrey. Recapture of these specimens might give information concerning their migratory habits or prove them capable of overwintering in Britain.

288. T[urner], H. J. (1937). "A few random thoughts on mass movement of Lepidoptera or pseudo-migration." Ent. Rec. 49: 70–1.

Considers the term migration unsuitable for non-vertebrate orders, and that "the vast majority of the records" are "bald, naked, simple facts of occurrence, unconnected observations and are practically useless".

289. Allan, P. B. M. (1937). "Some notes on assembling moths." Ent. Rec. 49: 66–9.

Attraction of three male *Saturnia pavonia* and three male *Notodonta dromedarius* to "calling" females in a district where the first named species had only twice been observed in the past 30 years, and the second was previously unknown; suggests that many male moths only pair once and that the female *S. pavonia* flies some distance between the phases of ovipositing.

290. Dannreuther, T. (1937). "Migration Records, 1936." Entomologist, 70: 5–10.

Contains a general summary of insect records in 1936. Further references by same author, ibid.: 92–3, 108–10, 141; **W. M. Christy**, ibid.: 114.

291. Burkill, H. J. (1937). "British butterflies in 1936." London Nat. for 1936: 48–50.

Little immigration: a few cases recorded here. Scattered notes on occurrence and abundance of several species in various parts of Britain.

292. Garrett, F. C. (1937). "Migrant Lepidoptera in 1936." Vasculum, 23: 37–8.

Migrants were unusually rare in the early summer, and although there was some improvement after midsummer they were generally scarce in the North-east of England.

293. Hodgson, S. B. (1937). "Abundance of the silver-Y moth (*Plusia gamma*) in West Hertfordshire, 1936." Trans. Herts. Nat. Hist. Soc. Fld. Cl. 20: 154–5.

This species showed a marked increase in September, possibly connected with a similar abundance late in August on the south and south-east coasts.

294. Hodgson, S. B. (1936). "The comma butterfly (*Polygonia c-album*) in Hertfordshire." Trans. Herts. Nat. Hist. Soc. and Fld. Cl. 20: 43–6.

This species used to be generally distributed in England, but then became very scarce except in some western counties. Since about 1919 it began to appear again in Hertfordshire, for which 60 records are given. These suggest that it has been spreading in from Buckinghamshire.

295. Dent, G. (1937). "Nature-notes from Harlow etc." Essex Nat. 25: 209.

Comma butterfly (*Polygonia c-album*) in Essex, continuing eastward spread.

296. Hodgson, S. B. (1936). "The white admiral butterfly in Hertfordshire." Trans. Herts. Nat. Hist. Soc. Fld. Cl. 20: 89.

This species (*Limenitis camilla*) has recently extended its range in southern England, and has now appeared in Herts.

297. Wilson, G. Fox (1937). "Contributions from the Wisley Laboratory. 80. A leaf-hopper (Jassid) on *Rhododendron*." J. R. Hort. Soc. 62: 210–13.

A North American Jassid, *Graphocephala coccinea* Forster, has recently been introduced and is well established on *Rhododendron* in some parts of Surrey. It is not yet known to be a pest, but in its natural country goes on several other plants, including strawberry.

298. Thompson, P. (1937). "Some tenants of banana-crates." Essex Nat. 25: 208–9.

Records following tropical animals found on arrival at docks and markets in West Ham, London: centipede, millipede, spiders, scorpion, cockroaches, cricket, beetle, butterfly, snail, snake, of which the names are given. The West Indian night mouse is common on banana ships.

8. REPORTS OF ORGANIZATIONS

The following reports include summaries of ecological work, some of the more important of which is noticed elsewhere. Purely preliminary summaries without full data or references are not noticed.

299. Avon Biological Research (1937). Annual Report, No. 4, 1935–6. (University College, Southampton. Price 2*s*. 6*d*.)

Research centring on the Avon as a salmon river, but also dealing with other fish, and their environment.

300. Bureau of Animal Population, Oxford University (1936). Annual Report, 1935–6. 48 pp.

Research mainly on populations of wild mammals and game-birds. Includes a list of recent literature on animal populations, which can be obtained free from the Bureau. The report is not on sale, but goes to many libraries, etc. (Secretary, Bureau of Animal Population, University Museum, Oxford.)

301. Freshwater Biological Association of the British Empire (1937). Fifth Report of Council. . . for year ending 31st March, 1937. 68 pp.

Research on freshwater animal and plant ecology in the Lake District. Issued to members of the Association, to which the minimum annual subscription is £1. 1*s*. (Dr E. B. Worthington, Wray Castle, Ambleside, Westmoreland.)

302. British Trust for Ornithology (1937). Third Report. 37 pp.

Research on the biology and ecology of birds. Issued to members of the Trust, to which the minimum subscription is 10*s*. (E. M. Nicholson, 61 Marsham St, London, S.W. 1.)

303. Lancashire and Cheshire Fauna Committee (1936). Twenty-second Annual Report and Report of the Recorders for 1935. 50 pp.

Deals mainly with local distribution records, in which are included habitat data, etc.

304. Committee on Bird Sanctuaries in Royal Parks (England) (1937). "Report for 1936." (H.M. Stationery Office, London. Price 9*d*.)

Contains a large number of unrelated but interesting notes on birds seen in the Royal Parks in and around London, including evidence of a pair of kestrels nesting on the Houses of Parliament.

305. Skokholm Bird Observatory (1936). Report for 1936. 11 pp.

Census records; and ringing work done at a bird live-trapping station set up in 1935. Eight Soay sheep were put on to the island. The report contains an attractive folder with line drawings of various sea-birds, mostly in flight; and information about the facilities for research on the island. (R. M. Lockely, Dale, Haverfordwest, Pembrokeshire.)

306. Anon. (1933). "The Tile Hill Nature Reserve: a review of the Society's second year of work." Proc. Coventry Nat. Hist. Sci. Soc. 1: 56–7.

In 1930 Coventry City Council set aside Tile Hill Wood as a Nature Reserve. The Society has been undertaking control and investigation of flora and fauna. The wood is about 80 acres, oak, conifer, birch, with pools and scrub as well. The Proceedings of the Society for the years 1930–7 contain a number of reports, including the introduction of fishes and certain plants; also surveys of the woodland flora and fauna including fungi, birds and insects.

9. BIBLIOGRAPHY

307. The South-Eastern Naturalist and Antiquary (1936). Index to the Transactions of the South-Eastern Union of Scientific Societies. Vols. 1–40. 1896 to 1935.

A useful subject index.

CAMBRIDGE: PRINTED BY W. LEWIS, M.A., AT THE UNIVERSITY PRESS